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Trophic Structure of the Eastern Chukchi Sea: An Updated Mass Balance Food Web Model

by
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ABSTRACT

This is a 2010s update of the previous 1990s Ecopath trophic mass balance model of the eastern Chukchi Sea. In the time since the original 1990s model was developed, a number of datasets have been produced and several reports and journal articles published documenting the findings of recent field studies in the eastern Chukchi Sea, including the completion of the BOEM-funded Arctic Ecosystem Integrated Survey (Arctic Eis). In this report we use published and unpublished datasets from many of these recent studies to update several input parameters from the preliminary 1990s Ecopath model of eastern Chukchi Sea, so it is more representative of the current (2010s) state of the eastern Chukchi Sea food web. Overall, 93 input parameters were updated and the data quality was improved for 34 parameters. A total of 9 new functional groups were added, 6 for seabirds and 3 for fish. Here we document all model parameters that we were able to update with improved information, including estimates of biomass, production, consumption, and diet composition. Changes in the included species, the species composition of functional groups, and their related parameters resulted in higher biomass for marine mammals, seabirds, fish and zooplankton, and decreased biomass for benthic invertebrates, jellies, microbes, and phytoplankton. Additionally, we calculate several ecosystem-level metrics for both models and compare the results between the original model and our updated model. In both models, benthic invertebrates represent the dominant portion of total ecosystem biomass, and energy flow is dominated by benthic resources. Total energy flow, total production, total biomass, and net primary production decreased from the preliminary model to the updated model. A key result common to both the preliminary model and the updated model is that trawl-survey-derived estimates of demersal fish biomass were insufficient to balance the model. Fish biomass needed to be several times greater to meet the modeled trophic demand from predators. Changes in the ecosystem metrics are the reflection of the updated and improved (higher quality) model inputs, and do not necessarily reflect any change in ecosystem state between the two model time periods. Given the number of updated parameters and improved data quality in the updated model (2010s), we recommend using the updated model over the preliminary model (1990s) for future modeling studies and as a baseline of this system’s food web.

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INTRODUCTION

The effects of climate change and sea ice decline are becoming increasingly apparent in the Arctic, with the nine lowest annual sea ice minima over the satellite record (1979-present) occurring in the last nine years, 2007-2015 (Comiso 2012, Stroeve et al. 2012, http://nsidc.org). Evidence of climate impacts on Arctic marine ecosystems is accumulating (Wassmann et al. 2011) and these systems may face additional stresses from increasing anthropogenic activity due to easier access following sea ice declines. The continental shelves of the Arctic possess large petroleum reserves (Gautier et al. 2009) and industrial activities related to petroleum extraction are expected to increase in the Alaska Arctic (Shell Gulf of Mexico Inc. 2015). In response, several intensive ecological investigations of oil and gas lease sites in the Alaska Arctic have recently been undertaken (Day et al. 2013, Dunton et al. 2014). The recent declines in sea ice coverage have also helped to increase interest in establishing new shipping lanes through the Arctic (Ho 2010, Lasserre and Pelletier 2011, Smith and Stephenson 2013), and prompted research on the impacts this vessel traffic may have on Arctic ecosystems (Jing et al. 2012, Reeves et al. 2012). Interest in Arctic tourism has also risen and related vessel traffic may increase as well in the near future (Williams 2014). What the cumulative impacts of climate change and increasing commercial development will be on Arctic marine ecosystems is unknown, but will likely be important. The Arctic is home to several species of marine mammals and fishes that are important resources for indigenous and non-indigenous residents of the Arctic (Craig 1987, Hovelsrud et al. 2008, Zeller et al. 2011). At present in the Alaska Arctic, the development of new commercial fisheries is prohibited until such a time that a sufficient amount of research and data become available to support the sustainable management of new commercial fisheries (NPFMC 2009). In consideration of the multiple, and potentially conflicting human interests in the Arctic marine environment, there is a growing need to provide stakeholders, resource managers, and decision makers with sufficient information to support an ecosystem-based approach to managing Arctic resources (Clement et al. 2013).

Ecosystem models are an effective tool in support of an ecosystem-based approach to managing marine resources (Christensen and Walters 2004, Link et al. 2012) and can be used to investigate ecosystem scale processes and the relative effects different stressors may have on ecosystems (e.g., Gaichas et al.

2011). An ecosystem model is a plausible representation of an ecosystem, or an ecosystem process, that can be used to make comparisons with real world observations and be used to evaluate hypotheses (Hilborn and Mangel 1997). Ecosystem models permit the user to conduct experiments that would otherwise be impractical in the real world, such as the manipulation of mortality rates or the strength of predator-prey interactions (e.g., Harvey et al. 2012). The results and insights from such exercises may provide valuable strategic guidance for resource managers and stakeholders (Samhouri et al. 2009).

A mass balance ecosystem model describing the food web of the eastern Chukchi Sea in Alaska has previously been developed. Whitehouse (2013) (hereinafter referred to as W13) compiled information on biomass levels, diet composition, rates for production and consumption, and harvest/fishery removals, and used this information to develop an Ecopath trophic mass balance model (http://ecopath.org/, Christensen and Pauly 1992) of the eastern Chukchi Sea. Whitehouse et al. (2014) used this model to describe the general structure and function of this ecosystem. They found the ecosystem to be dominated in terms of biomass by benthic invertebrates and found that the majority of mass flows amongst consumer groups (trophic level ≥ 2.0) were through benthic oriented organisms as opposed to pelagic organisms (e.g., zooplankton). Additionally, they found that biomass estimates of fish groups, derived from trawl survey data, were insufficient to meet the trophic demands from predators and, thus, trawl surveys were likely underestimating fish densities.

The preliminary mass balance food web model of the eastern Chukchi Sea was constructed in an effort to provide a comprehensive view of the ecosystem using the data and rates available at that time, primarily centered on the years surrounding 1990, as many of the data needed to parameterize the preliminary model were available from that time period. Having a base time period of 1990 was an important limitation of this preliminary model, given the more recent observations of shrinking and thinning sea ice coverage. It is not clear whether food web conditions in the Chukchi Sea have undergone any changes since the 1990s. In the time since the preliminary model was developed a number of interdisciplinary ecological studies of the Chukchi Sea have been completed and published, adding to the knowledge about this ecosystem (e.g., Bluhm et al. 2010 [RUSALCA], Day et al. 2013 [CSESP], Dunton et al. 2014 [COMIDA-CAB]). The Arctic Ecosystem Integrated Survey (Arctic Eis, https://web.sfos.uaf.edu/wordpress/arcticeis/) is continuing to build upon this growing knowledge base by conducting a comprehensive assessment of the oceanography, plankton, and fishes of the northern Bering Sea and Chukchi Sea. The information collected during the Arctic Eis will help enable resource managers to evaluate the potential effects of climate and human activities on this ecosystem.

In this study we improved upon the preliminary food web model by incorporating data and information from recent studies to more closely represent the current ecological conditions in the eastern Chukchi Sea. Specifically, we incorporated data gathered during the BOEM-funded Arctic Eis, including updated biomass estimates of trawl-caught organisms and the diet composition of fishes. Additionally, we updated other model parameters where current or otherwise improved estimates were available in the literature. We compare the original and updated models, examined how the new data and rates may have affected model outputs, and discuss whether any changes in ecosystem properties may be a reflection of the new data or of actual changes in ecological conditions.

METHODS

Study System

The Chukchi Sea is a marginal Arctic Sea that is seasonally covered by ice. The broad and shallow continental shelf, with most depths shallower than 60 meters (Jakobsson 2002), is the only connection between the Pacific and Arctic oceans (Carmack and Wassmann 2006). The Chukchi Sea has a strong advective regime, in which a net northward flow of Pacific origin water passes through the Bering Strait and continues in a net northward direction across its continental shelf (Coachman et al. 1975, Roach et al. 1995, Weingartner et al. 2005, Woodgate et al. 2005). The Pacific origin water flowing into the Chukchi Sea is rich with nutrients and fuels high levels of primary production throughout the ice free season, particularly in the southern Chukchi Sea (Sambrotto et al. 1984, Hansell and Goering 1990, Springer and McRoy 1993). Only a small portion of the primary production is consumed by zooplankton (Cooney and Coyle 1982, Coyle and Cooney 1988, Campbell et al. 2009, Sherr et al. 2009) and most of it eventually sinks out of the water column to the sea floor, where it supports an abundant benthic food web (Grebmeier et al. 1988, Dunton et al. 2005). The thriving benthic community in turn supports benthic foraging specialists including gray whales (*Eschrichtius robustus*), Pacific walrus (*Odobenus rosmarus*), and bearded seals (*Erignathus barbatus*). Several marine mammal species are regular occupants of the Chukchi Sea and many of these species, such as bowhead whales (*Balaena mysticetus*) and ringed seals (*Phoca hispida*), are important subsistence resources for the residents of Alaska coastal villages (Hovelsrud et al. 2008).

The Chukchi Sea is an international sea, shared by the United States and the Russian Federation, and is approximately bisected by the U.S.-Russia Maritime Boundary. We focused our study on the eastern Chukchi Sea within the territorial waters of the U.S. There is no ecosystem basis for modeling only the eastern Chukchi Sea. This decision is a reflection of the general unavailability of datasets providing an adequate description of the western Chukchi Sea, and we felt it was inappropriate to extrapolate our parameters for the eastern region to the entire extent of the Chukchi Sea. The model describes the continental shelf waters of the eastern Chukchi Sea between the 20 m and 70 m isobaths, covering approximately 192,000 km^{-2} (Fig. 1). Waters outside this depth boundary are beyond the range of most trawl surveys and may incorporate nearshore and deep-water processes and species that are not included in this or the original model. The only exception to the 70 m depth limit is the portion of Barrow Canyon north and west of Pt. Barrow, where the maximum depth is approximately 150 m. The model area is bordered by the Bering Strait to the south, Pt. Barrow to the east, the U.S. Russia Maritime Boundary to the west, and a combination of the U.S. Exclusive Economic Zone (EEZ, 200-mile limit) and 70 m isobath to the north. Near shore the model is bounded by the 20 m isobath.

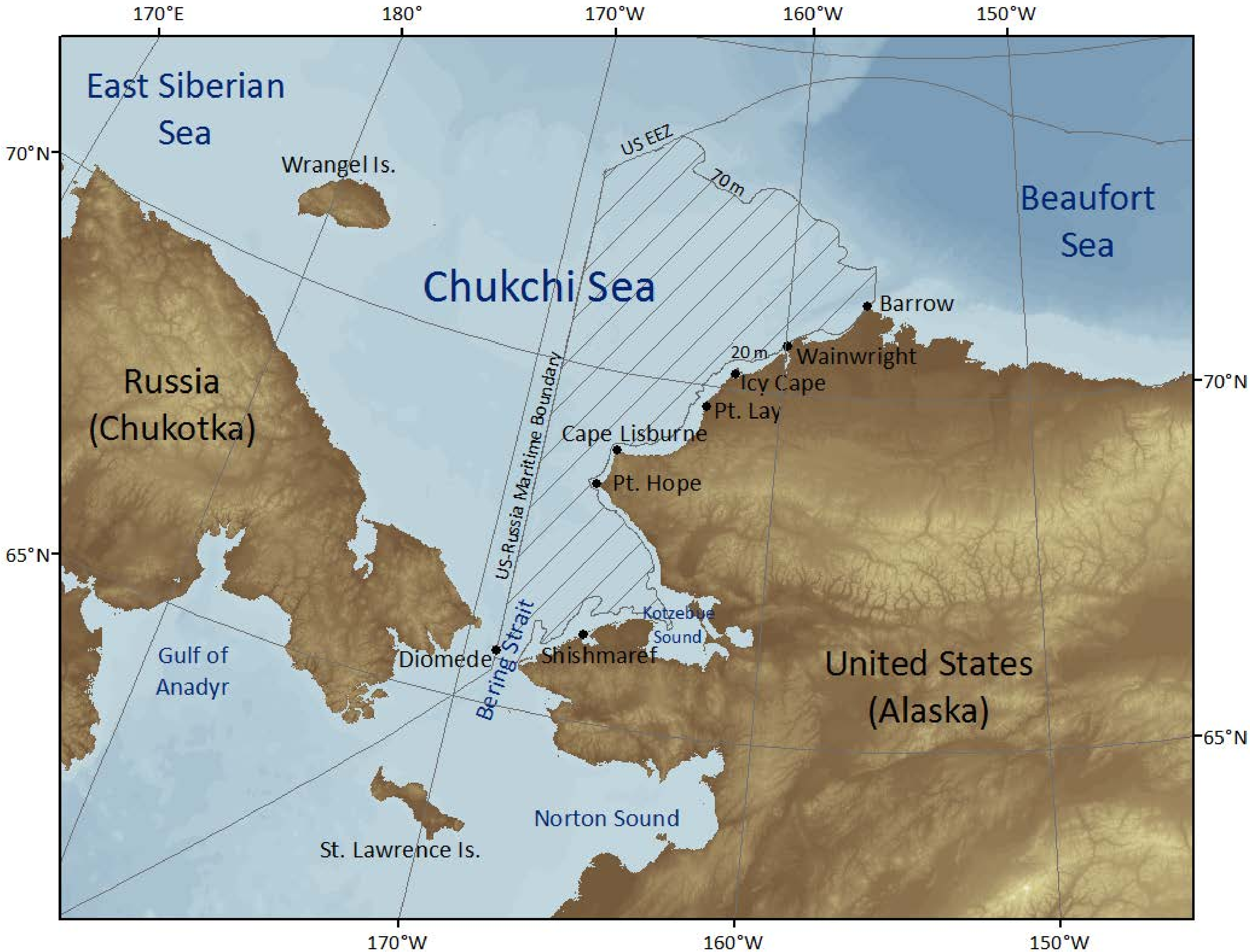

Figure 1. -- The model area in the eastern Chukchi Sea (filled with hatched lines).

General Methodology for the Model Update

The primary purpose of this report is to update the existing preliminary trophic mass balance model of the eastern Chukchi Sea (W13) so that it better represents current conditions in this ecosystem. The preliminary model had a base time period of the early 1990s because much of the data needed to parameterize the preliminary model was available from that time period, even though some more recent parameter values may have been available. This model update revised many of the model parameter values by incorporating data from more recent studies, so as to provide a more accurate and current representation of the eastern Chukchi Sea food web. Primarily we will be incorporating data gathered as part of the BOEM-funded Arctic Eis trawl surveys of the eastern Chukchi Sea during the summer of 2012. Additionally, we have updated other model parameters as data permitted and as required by the model balancing process.

Modeling Framework

Using the Ecopath with Ecosim (EwE, version 6) modeling framework (Christensen et al. 2008), we update the earlier eastern Chukchi Sea model. Ecopath is a static, mass balance food web model originally developed by Polovina (1984) to describe a coral reef ecosystem and has since been used to study ecosystems around the globe, including high latitude marine ecosystems (e.g., Cornejo-Donoso and Antezana 2008, Pedersen et al. 2008, Gaichas et al. 2009, Morissette et al. 2009, Whitehouse et al. 2014, Lovvorn et al. 2015). Ecopath is a biomass compartment model where each compartment represents a species or functional group of multiple species and describes the material flows between compartments in a food web. The mass balance requirement ensures that production by a compartment is sufficient to match removals by predators and fisheries catch. The balanced model provides a snapshot of ecosystem structure and can be used to calculate a number of metrics which describe key ecosystem attributes. Under equilibrium conditions, the interactions between functional groups are described by a set of linear equations. For each group (*i*) with predators (*j*), this relationship is expressed as:

$$B_i\left(\frac{P}{B}\right)_i * EE_i = \sum_j B_j * \left(\frac{Q}{B}\right)_j * DC_{ij} - C_i\ , \tag{1}$$

where B is biomass density (t km^{-2}) in wet weight, P/B (yr^{-1}) is the production to biomass ratio, Q/B (yr^{-1}) is the consumption to biomass ratio, DC_{ij} is the proportion of prey *i* in the diet of predator *j*, and C is subsistence harvest or fisheries catch (t km^{-2}) of group *i*. Ecotrophic Efficiency (EE) is the proportion of production (B_i*$[P/B]_i$) that is consumed by predators and removed by fisheries/subsistence harvests included in the model and must be ≤ 1.

Mass balance is achieved by solving this set of linear equations for one missing parameter for each functional group. DC must be entered into the model and typically B, P/B, Q/B, and C are also entered, and the equation is solved for EE. When reliable estimates of model parameters are unavailable, EE can be set to an arbitrary value and the equation solved for the missing parameter. This is usually done for B, and is commonly referred to as a “top-down balance” because the model is estimating biomass based on top-down removals from predators and fisheries. EE is difficult to measure in nature and is generally unknown but is thought to be close to 1 for prey groups subject to heavy predation and/or fishing pressure and close to zero for top predators that experience little predation and fishing pressure (Christensen et al. 2005). All top-down balancing performed in the original model was done with EE set to 0.8, and for consistency, we take the same approach here. Setting EE to 0.8 implies that the model explains 80% of the total mortality through the predation and fisheries removals explicitly included in the model. Other sources of mortality not included in the model but accounting for the remaining 20% of total mortality (1-EE) include disease, senescence, starvation, and possible outmigration. This non-predation mortality is generally not measurable, and applying a uniform percentage to this unexplained mortality (20%) allows for a standardized analysis and is generally consistent with dynamic fits of unexplained mortality across a range of species (Aydin et al. 2007).

The energy balance within a functional group must also be maintained, and the total production, plus the costs for maintenance and metabolism (respiration), plus the fraction of food that is not assimilated, must not exceed their total consumption. This is ensured for each functional group *i* with the following equation:

$$Q_i = P_i + R_i + U_i \ , \tag{2}$$

where Q_i is total consumption (i.e., B_i*[Q/B]$_i$), P_i is total production (i.e., B_i*[P/B]$_i$), R_i is respiration, and U_i is the portion of consumption that is unassimilated and is egested or excreted as feces and urine, and is directed to detritus. Estimates of Q, P, and U are generally more available than R, thus equation 2 is used to estimate R. Measurements of the portion of consumed food that is unassimilated (i.e., 1-assimilation efficiency) are highly variable, and are influenced by biological and environmental factors including the predator species, prey quality, the amount consumed, temperature, and gut passage time (Winberg 1960, Conover 1966, Bayne et al. 1988, Gaudy et al. 1991, Hop et al. 1997, Bochdansky et al. 1999). We use the default value of 0.2 for the unassimilated fraction of food (U/Q) for most functional groups, meaning 20% of total consumption is not useful for production or respiration (Christensen et al. 2008). For benthic detritivores (DC at least 50% benthic detritus) the unassimilated fraction is assumed to be higher (Welch 1968) and we use a default of 0.4 (Christensen et al. 2008).

Model balancing is the process of solving the system of linear equations set up by Ecopath to ensure mass balance is achieved. Normally, initial attempts to balance an Ecopath model are unsuccessful and a number of functional groups will be out of balance (EE > 1). This sometimes alerts the model developer to an error that may have been made during model development (e.g., misplaced decimal point, typo, etc.), but more often highlights instances where a collection of the model inputs are incompatible (e.g., predator consumptive requirements in excess of prey production). When input parameters are determined to be incompatible, the parameters in question, and all related parameters, need to be re-evaluated to determine how to best reconcile the conflicting parameters. This can involve selecting a different parameter from the published literature or recalculating a parameter based on the new information, using Ecopath to solve for the parameter in doubt, making a manual adjustment to the input parameter value, or reconfiguring functional groups.

Data Sources and Data Quality

The development of an ecosystem-scale food web model necessitates the synthesis of a large body of literature and requires the inclusion of data and rates of varying quality, from a variety of sources. Some data and rates can be directly inserted to the model, while others may require some modification to account for the temporal and spatial limitations of the model framework. We graded all model parameters and/or data for quality and uncertainty using a data pedigree previously described by Christensen et al. (2005), with specific data quality definitions from Aydin et al. (2007). Model parameters and data were assigned a data pedigree (grade) based upon the data source, collection methodology, temporal and spatial coverage of the dataset, and taxonomic relevance.

In this model update, we used the same data pedigree (Table 1) as that used in the development of the preliminary model (W13). Where input parameters (B, P/B, Q/B, DC, C) have been updated for the current analysis, we have provided in the Results section a detailed description of parameter development, data sources, and parameter adjustments. Parameters from the preliminary model that remain unadjusted in the updated model will not be described in detail here, and instead the reader is referred to the preliminary model documentation (W13). The full suite of basic model parameters is presented in Table 2 and the diet matrix can be found in Appendix A. Input parameters that have been updated from the original model are highlighted with red text in Table 2. Additionally, the data pedigree for basic model parameters can be found in Appendix B.

Table 1. -- The criteria for the data pedigrees (or data quality grade). B = biomass, P/B = production/biomass ratio, Q/B = consumption/biomass ratio, DC = diet composition, and C = fishery catch or subsistence harvest. (This table recreated from Aydin et al. 2007).

	Data pedigree and corresponding data characteristics
	B, P/B, Q/B, DC, and C
1	Assessment data is established and substantial, from more than one independent method (from which the best method is selected) with resolution on multiple spatial scales.
2	Data is a direct estimate but with limited coverage/corroboration, or established regional estimate is available while subregional resolution is poor.
3	Data is proxy, proxy may have known but consistent bias.
4	Direct estimate or proxy with high variation/limited confidence or incomplete coverage.

	B and C		**P/B, Q/B, and DC**
5	Estimate requires inclusion of highly uncertain scaling factors or extrapolation	5	Estimation based on same species but in "historical" time period, or a general model specific to the area.
6	Historical and/or single study only, not overlapping in area or time.	6	For P/B and Q/B, general life history proxies or other Ecopath model. For DC, same species in adjacent region or similar species in the same region.
7	Requires selection between multiple incomplete sources with wide range.	7	General literature review from a wide range of species, or outside the region. For DC, from other Ecopath model.
8	Estimated by Ecopath	8	Functional group represents multiple species with diverse life history traits. For P/B and Q/B, estimated by Ecopath.

Table 2. -- (Next page). The basic model parameters for the updated eastern Chukchi Sea Ecopath model. Parameters that are input to the model are in bold and italicized. Input parameter values that are different from the preliminary model are additionally highlighted in red. New functional groups added to the updated model are also highlighted in red. TL is Trophic Level, B is Biomass, P/B is production to biomass ratio, Q/B is consumption to biomass ratio, EE is ecotrophic efficiency, GE is growth efficiency, and U/Q is the unassimilated fraction of consumed food. B is in t km^{-2}; P/B, Q/B, and GE are in $year^{-1}$, and EE and U/Q are dimensionless.

Table 2. -- Cont.

Group	TL	B	P/B	Q/B	EE	GE	U/Q	Removals
Beluga	4.6	0.01159	0.11	14.50	0.211	0.008	0.2	6.34E-05
Gray whale	3.5	0.18795	0.06	8.87	0.000	0.007	0.2	
Bowhead whale	3.5	0.39848	0.01	5.26	0.299	0.002	0.2	0.00120
Polar Bear Chukchi	5.5	0.00040	0.06	4.00	0.663	0.015	0.2	1.61E-05
Polar Bear S Beaufort	5.5	0.00012	0.06	4.00	0.304	0.015	0.2	2.26E-06
Pacific walrus	3.4	0.05909	0.07	21.66	0.757	0.003	0.2	0.00308
Bearded seal	3.9	0.03905	0.08	12.94	0.912	0.006	0.2	0.00177
Ringed seal	4.7	0.05587	0.09	19.23	0.896	0.005	0.2	0.00212
Spotted seal	4.8	0.00579	0.07	18.70	0.385	0.004	0.2	0.00015
Procellarids	3.7	0.00193	0.07	187.93	0.000	0.0004	0.2	
Cormorants	4.4	1.47E-06	0.16	142.62	0.000	0.001	0.2	
Scolopacids	3.5	7.77E-05	0.16	374.31	0.000	0.0004	0.2	
Larids	4.5	9.31E-05	0.11	205.67	0.000	0.001	0.2	
Alcids piscivorous	4.8	0.00116	0.10	178.38	0.741	0.001	0.2	
Alcids planktivorous	3.5	0.00014	0.14	247.51	0.000	0.001	0.2	
Large-mouth flatfish	4.2	0.11142	0.40	1.78	0.800	0.225	0.2	
Small-mouth flatfish	3.4	0.09015	0.31	1.54	0.800	0.201	0.2	
Large-mouth sculpin	4.3	0.59984	0.40	2.00	0.800	0.200	0.2	
Other sculpin	3.6	0.85526	0.46	2.42	0.800	0.190	0.2	
Eelpout	3.7	0.38218	0.40	2.00	0.800	0.200	0.2	
Pelagic forage fish	3.7	1.19059	0.54	2.92	0.800	0.186	0.2	
Misc. shallow fish	3.5	6.49835	0.40	2.00	0.800	0.200	0.2	
Other snailfish	3.8	0.13509	0.40	2.00	0.800	0.200	0.2	
Variegated snailfish	4.3	0.09874	0.40	2.00	0.800	0.200	0.2	
Alaska skate	4.4	0.00536	0.21	2.10	0.000	0.100	0.2	
Walleye pollock	4.2	0.00054	0.87	3.01	0.0001	0.289	0.2	
Pacific cod	4.0	3.79E-05	0.55	2.80	0.744	0.195	0.2	
Saffron cod	4.0	0.97905	0.55	2.80	0.800	0.195	0.2	
Arctic cod	3.7	1.04491	0.87	3.01	0.800	0.289	0.2	
Salmon outgoing	3.5	0.00052	1.28	13.56	0.000	0.094	0.2	
Salmon returning	3.5	0.00521	1.65	11.60	0.027	0.142	0.2	
Cephalopods	3.9	0.01058	1.77	8.85	0.800	0.200	0.2	
Bivalves	2.3	90.28777	0.76	3.78	0.289	0.200	0.4	
Snails	3.3	1.38446	1.77	8.85	0.254	0.200	0.2	
Snow crab	3.1	3.16997	1.00	2.75	0.082	0.364	0.2	
Other crabs	3.1	3.06715	0.82	4.10	0.330	0.200	0.2	
Shrimps	2.9	7.49216	0.58	2.41	0.800	0.239	0.2	
Sea stars	3.3	2.18016	0.34	1.70	0.032	0.200	0.2	
Brittle stars	2.7	5.64425	0.49	2.43	0.197	0.200	0.4	
Basket stars	3.5	0.50986	0.34	1.70	0.002	0.200	0.2	
Urchins, dollars, cucumbers	2.0	36.28965	0.70	3.48	0.050	0.200	0.4	
Sponges	2.3	0.52716	1.00	5.00	0.047	0.200	0.4	
Benthic urochordates	2.3	1.16008	3.58	17.90	0.033	0.200	0.4	
Anemones	3.1	0.38413	1.00	5.00	0.387	0.200	0.2	
Corals	2.3	0.02568	0.05	0.23	0.006	0.200	0.4	
Benthic amphipods	2.5	20.52616	1.00	5.00	0.800	0.200	0.4	
Polychaetes	2.5	27.80796	2.92	14.58	0.209	0.200	0.4	
Worms etc.	2.5	17.03959	2.23	11.15	0.119	0.200	0.4	
Misc. crustaceans	2.5	5.58099	2.01	10.04	0.617	0.200	0.4	
Jellyfish	3.4	0.37197	0.88	3.00	0.002	0.293	0.2	
Copepods	2.5	2.04268	6.00	27.74	0.800	0.216	0.2	
Other zooplankton	2.5	1.22520	5.48	15.64	0.800	0.350	0.2	
Pelagic microbes	2.0	1.48870	26.25	75.00	0.800	0.350	0.2	
Benthic microbes	2.0	22.31165	26.25	75.00	0.800	0.350	0.2	
Phytoplankton	1.0	27.8	75.00		0.072			
Pelagic detritus	1.0	1427.98			0.047			
Benthic detritus	1.0	4879.12			0.9997			

Cetaceans

We include the dominant and most frequently observed species of cetaceans known to reside for some portion of the year in the eastern Chukchi Sea. Though other cetacean species have been sighted in the region on several occasions (e.g., humpback whale, fin whale, minke whale, killer whale; see Clarke et al. 2013) we only include those species for which the eastern Chukchi Sea comprised a well-established portion of their current range.

Changes to the parameters for cetacean groups are primarily updates from the historical abundance estimates to the most recent abundance estimates available. There were no changes to P/B, Q/B, or diet composition. For the model parameters not modified as a part of this model update (B, P/B, Q/B, DC, C), detailed functional group descriptions, including data sources, any parameter adjustments, and the diet matrix can be found in the preliminary model documentation (W13). We do provide a brief summary here of the methods used in the preliminary model for parameter development.

Biomass (B)

The biomass density estimates of cetacean groups were calculated from published estimates of abundance, average individual body mass, and information regarding migration and seasonal occupancy of the eastern Chukchi Sea. Due to the seasonal sea ice coverage and known migration patterns of cetaceans, the abundance and biomass estimates were lowered to reflect time spent within the model area only. The general formula to calculate cetacean biomass density (t km^{-2}) for the model is to multiply population abundance estimates by published estimates of species-specific average individual body mass (Hunt et al. 2000), then reduce this biomass estimate by multiplying it by the proportion that reflects the amount of time within a year spent within the model area, and finally divide this corrected biomass by the model area (km^2). This results in a density estimate (B) in t km^{-2}.

Production (P/B)

The P/B ratios for cetaceans in this updated model are the same as those in the preliminary model. The P/Bs for cetaceans in the preliminary model were estimated with a variation of Siler's competing risk model (Siler 1979) as modified by Barlow and Boveng (1991). Under equilibrium conditions, P/B is assumed to be equal to the instantaneous mortality rate, Z (Allen 1971). This method uses surrogate life histories scaled by longevity to produce survivorship curves, which are used to estimate P/B.

Consumption (Q/B)

The cetacean Q/Bs used in this model update are unchanged from the values used in the preliminary model. Q/Bs were calculated using a generalized formula for calculating marine mammal daily energy requirements from Perez et al. (1990) and scaled up to an annual rate. Estimates of prey caloric density and average individual body mass were taken from Hunt et al. (2000).

Food habits (DC)

The diet compositions of cetacean groups are taken from a variety of literature sources.

Caniforms

The caniforms includes two stocks of polar bears (*Ursus maritimus*) and four species of pinnipeds, the Pacific walrus (*Odobenus rosmarus*), bearded seal (*Erignathus barbatus*), ringed seal (*Phoca hispida*), and spotted seal (*P. largha*). This group is limited to caniform species whose established range includes the eastern Chukchi Sea for some portion of the year. Ribbon seals (*Histriophoca fasciata*) in particular, were not included as only a small number of ribbon seals are thought to migrate north through Bering Strait (Burns 1970, 1981a, Boveng et al. 2008) and they are infrequently spotted near coastal villages in the southern Chukchi Sea, with sightings in the northern Chukchi Sea being rare (Burns 1981a).

Current or improved estimates of biomass are not presently available for polar bears or most ice-associated pinnipeds in the eastern Chukchi Sea. Biomass is only updated for Pacific walrus. There were no changes to P/B or Q/B for any of the caniforms, however we do summarize here the methodology used in the preliminary model to estimate these parameters. Diet composition was modified for bearded seals and spotted seals, reflecting changes in the species composition of fish functional groups. See the preliminary model documentation (W13) for detailed descriptions of caniform functional groups, including the development of model parameters that were not modified as a part of this model update (B, P/B, Q/B, DC, C), data sources, and any parameter adjustments.

Biomass (B)

The biomass density estimates of caniform functional groups were calculated based on published species-specific abundance estimates, estimates of mean body mass (Derocher 1991, Trites and Pauly 1998), as well as data and information regarding migration, seasonal distribution, and time spent in the eastern Chukchi Sea. Due to the seasonal sea ice coverage and pinniped migration patterns, biomass estimates were lowered as needed to reflect the seasonal nature of their occupation of the model area. The general formula for caniform biomass density (t km^{-2}) is to multiply the abundance estimate by a species-specific mean body mass, then multiply this number by the proportion of time in one year spent occupying the model area. Finally, the biomass (t) is divided by the model area (km^{-2}) to result in the biomass density estimate.

Production (P/B)

The P/Bs for pinniped groups were estimated in the preliminary model (W13) with a variation of Siler's competing risk model (Siler 1979) as modified by Barlow and Boveng (1991). Under equilibrium conditions, P/B is assumed to be equal to the instantaneous mortality rate, Z (Allen 1971). This method uses surrogate life histories scaled by longevity to produce survivorship curves, which are used to estimate P/B. The P/Bs of the polar bear groups are approximated with an estimated annual intrinsic population growth rate for the southern Beaufort Sea stock of polar bears (Amstrup 1995).

Consumption (Q/B)

Pinniped Q/Bs are estimated with a generalized formula from Perez et al. (1990) for calculating marine mammal energy requirements, and scaling up to an annual rate. Estimates of pinniped average individual body mass are from Trites and Pauly (1998), and estimates of prey caloric density are from Hunt et al. (2000). The polar bear Q/Bs are estimated using the basal metabolic rate from Best (1977), prey caloric density from Stirling and McEwan (1975), and with information on individual body mass from Derocher (1991).

Food habits (DC)

The diet compositions of caniform groups are derived from a variety of literature sources. The diet compositions of bearded seals and spotted seals were not updated but were modified to conform to the reconfiguration of some fish functional groups. Bering flounder was moved from the small-mouth flatfish group and added to the large-mouth flatfish group. This is relevant to bearded and spotted seals because flatfish have been identified as part of their diets (Lowry et al. 1980a, Burns and Frost 1983, Lowry et al. 1983, Bukhtiyarov et al. 1984, Perez 1990, Dehn et al. 2007); however, species level identifications of flatfish prey are not available. Lacking species-specific information, we decided to evenly proportion the amount of flatfish consumed by bearded and spotted seals between the small and large-mouth flatfish groups.

Seabirds

We focused on the dominant and most frequently observed seabirds of the eastern Chukchi Sea, for which the pelagic environment is their primary habitat. We recognize the presence of many other bird species that make use of the pelagic environment of the eastern Chukchi Sea (> 20m depth) as regular transients or occasional visitors but have a different primary habitat, such as waterfowl (e.g., eiders, loons, scoters, etc.) and shorebirds (e.g., sandpipers, dowitchers, etc.); we have excluded these species from the analysis. There are 6 total functional groups representing 20 species of seabirds.

New seabird functional groups

In this model update we include an additional 8 species of seabirds and maintain the same number of seabird functional groups-6 from W13. To accomplish this we have reconfigured the seabird functional groups to reflect family relationships (e.g., Laridae, Procellaridae) or grouped by diet similarities within family (e.g., Alcids piscivorous, Alcids zooplanktivorous). A notable shortcoming of the seabird groups in the preliminary model (Whitehouse et al. 2014), was the omission of pelagic migrants and nonbreeders that do not occupy or maintain coastal colonies within the eastern Chukchi Sea region (e.g., short-tailed shearwaters [*Puffinus tenuirostris*], phalaropes [*Phalaropus* spp.]). These pelagic migrants may be among the most numerous birds found offshore in the Chukchi Sea during the ice-free season (Divoky 1987, Gall et al. 2013, Hunt et al. 2013). Therefore, we have added two new functional groups: 1) the Procellarids, which contains northern fulmars (*Fulmaris glacialis*) and short-tailed shearwater (*Puffinus tenuirostris*), and 2) the Scolopacids, which contains the red-necked phalarope (*Phalaropus lobatus*) and

Red phalarope (*P. fulicarius*). The complete reconfiguration of the seabird functional groups necessitated that all model input parameters were recalculated for all seabird functional groups.

Biomass (B)

The preferred method of calculating biomass density for seabirds was to use colony count data multiplied by individual species-specific body mass. Though colony count data may underestimate the abundance of seabirds in the area by not accounting for non-breeders, the colony counts are used here as a best conservative estimate of seabird abundance because it is assumed the colony counts reflect consistent annual occupation of the study area. A previous study of seabirds breeding in the northern Bering/southern Chukchi sea region found that species population estimates derived from colony counts were of similar orders of magnitude as pelagic estimates (Piatt and Springer 2003). However, using only colony data excludes pelagic migrants and non-breeders. To include these species in our current work necessitated the use of pelagic estimates of seabird density. In this model update we have attempted to include the most abundant pelagic migrants by utilizing unpublished population estimates of seabirds occupying the eastern Chukchi Sea during the period of maximum annual seabird abundance (late summer/early fall) (Divoky 1987). The regional scale of the estimates reported in Divoky (1987) effectively describe seabird use of the entire eastern Chukchi Sea (approximately equivalent to the total area described by our model, 192,054 km^2). This was seen as an advantage over more recent pelagic seabird density estimates focused on three oil and gas lease sites, covering only about 9,000 km^2 in the northeastern Chukchi Sea (Gall et al. 2013). The basic methods for the population estimates reported by Divoky (1987) are briefly reviewed here. Average seabird density estimates were derived from pelagic surveys that were conducted throughout the eastern Chukchi Sea from 1970 to 1986 on nine separate cruises during the ice-free season. The coarse population estimates reported in Divoky (1987) were calculated by multiplying the average seabird density (birds km^{-2}) for the study region by the total area (km^2) of the study region.

We calculated density estimates from the coarse population estimates of Divoky (1987) for Procellarids (northern fulmars and short-tailed shearwaters) and Scolopacids (red-necked phalarope and red phalarope). The population estimates were converted to biomass density estimates (t km^{-2}) by dividing the total population estimate by the total area of our study region, then multiplying by a species-specific mean body mass, taken from Hunt et al. (2000). Species-specific abundance estimates are not available for phalaropes, so a mean body mass for the two species is used. The biomass estimates were reduced further to accommodate the model's annual time frame and account for the birds' seasonal occupation of the model area (~ 4 months), by multiplying the density estimate times one-third.

Biomass estimates of nesting seabirds were derived from colony counts made at seabird colonies found within the model area and along the coast of Alaska between the model's southern boundary at Bering Strait (65°40' N) and eastern Boundary at Pt. Barrow (156°25' W). Colony counts of nesting seabirds were obtained from the North Pacific Seabird Colony Database (Seabird Information Network 2011), an online interactive database that contains current and historical records of censused seabird colonies in the north Pacific, including Alaska and the Russian Far East. In the previous edition of this food web model (W13), colony counts were obtained from a predecessor to the North Pacific Seabird Colony Database, the Beringian Seabird Colony Catalog (USFWS 2003).

The colony counts selected for use in this model were conducted over many years, from 1959 to 1998, by different observers, and to our knowledge are the most current and best colony counts available. The preferred method for calculating seabird biomass density was to multiply the total number of seabirds from the colony counts by the respective species-specific mean body mass found in Hunt et al. (2000). Biomass estimates were added together for species within the same functional group. The estimated biomass was then divided by the total model area to arrive at the functional group biomass density (t km^{-2}). The biomass density estimate was then reduced further to account for the model's annual time frame and the seabird's seasonal occupation of the model area (~4 months), by multiplying times one-third (Table 5).

Mean individual body masses were compiled from the literature by Hunt et al. (2000) for all species except the black guillemot (*Cepphus grylle*) and unidentified murres. The mean individual body mass for black guillemots was calculated as the average of male and female body masses reported by Berzins et al. (2009). The mean individual body mass used for unidentified murres is the average of the mean individual body masses for common murres and thick-billed murres, weighted by their estimated biomass within the study region.

Production (P/B)

There are few published estimates of P/B for seabirds. Because seabirds are largely unexploited we use estimated survival rates (S) in their place, and set P/B equal to the negative logarithm of the survival rate (P/B = -ln[S]). Species-specific survival rates were preferred but when they were unavailable an order level, average survival rate was used, except for puffins (Table 6). All survival rates are from Schreiber and Burger (2001). Where annual survival rates were given as a range, the midpoint of that range was used in calculations. Survival rates for horned and tufted puffins were unavailable, so in their place we use the Atlantic puffin (*Fratercula arctica*) survival rate. The functional group P/B is an average of the species-specific (and/or order level) P/Bs, weighted by biomass.

Consumption (Q/B)

Estimates of Q/B had to be developed for all seabird species due to the reconfiguration of the seabird functional groups. In the preliminary eastern Chukchi Sea model all estimates of seabird Q/B were taken from taxonomically equivalent functional groups in an Ecopath model of the eastern Bering Sea. A different approach is taken here and Q/B is calculated from daily allometric energy requirements for seabirds presented in Hunt et al. (2000). These daily energy requirements were calculated for each species individually using the allometric equation of Birt-Friesen et al. (1989):

$$\log Y = 3.24 + 0.727 * \log M \,, \tag{2}$$

where Y = the daily energy requirements in kj, and M is the body mass in kg.

The average prey energy density (kj g^{-1}) for generalized seabird prey groups has previously been described by Hunt et al. (2000). We determined the energy density of seabird prey in our model by assigning each prey functional groups to one of the generalized prey categories, with its corresponding energy density, described in Hunt et al. (2000) (Table 3). Average prey energy density was calculated for each predator as the average energy density weighted by the prey's proportion in the predator's diet. The functional group Q/B is an average Q/B weighted by the estimated biomass of the group's constituent species within the model area (Table 7).

Food habits (DC)

The diet compositions of seabirds are taken from a variety of literature sources. The diets of multi-species functional groups are an average diet weighted by biomass.

Table 3. -- Approximate energy density (kj g^{-1}) of functional groups found as prey in the diet of seabirds. Energy densities and corresponding prey categories are taken from Hunt et al. (2000).

Prey functional group	Prey category from Hunt et al. (2000)	energy density (kj/g)
Alcids piscivorous	Birds and mammals	7.0
Large-mouth flatfish	Fish low density	3.0
Small-mouth flatfish	Fish low density	3.0
Large-mouth sculpin	Fish low density	3.0
Other sculpin	Fish low density	3.0
Eelpout	Fish low density	3.0
Pelagic forage fish	Fish med density	5.0
Misc. shallow fish	Fish low density	3.0
Walleye pollock	Fish low density	3.0
Pacific cod	Fish low density	3.0
Saffron cod	Fish low density	3.0
Arctic cod	Fish low density	3.0
Snow crab	Misc. inverts	4.0
Bivalves	Misc. inverts	4.0
Snails	Misc. inverts	4.0
Crabs	Misc. inverts	4.0
Shrimps	Misc. inverts	4.0
Brittle stars	Misc. inverts	4.0
Urchins, dollars, cucumbers	Misc. inverts	4.0
Jellyfish	Gel. zooplankters	3.0
Cephalopods	Sm. cephalopods	3.5
Benthic amphipods	Misc. inverts	4.0
Polychaetes	Misc. inverts	4.0
Worms etc.	Misc. inverts	4.0
Misc. crustaceans	Misc. inverts	4.0
Copepods	Crust zoop	4.0
Other zooplankton	Crust zoop	4.0

Fish

In this model update the number of fish functional groups has expanded from 13 to 16. This expansion is a reflection of the catch data from the 2012 Arctic Eis bottom trawl survey and additionally, the result of incorporating updated region- and species-specific diet data for fishes, also collected during Arctic Eis trawl surveys (Whitehouse et al. In press). The biomass density and diet composition have been updated for all fish functional groups, except salmonids for which all parameters remain unchanged.

Biomass (B)

Initial fish biomass density estimates were derived from the catch data of the 2012 Arctic Eis bottom trawl survey of the eastern Chukchi Sea. The survey was conducted during August and September aboard the chartered fishing vessel Alaska Knight. The fish were sampled with an 83-112 Eastern bottom trawl (EBT) with 25.3 m headrope and 34.1 m foot rope with a 4.5 mm codend liner, towed for 15 min. at 3 knots. Station locations were determined using a systematic grid design with 30 x 30 nautical mile grid cells, and trawls were attempted at the center of each grid square. Bottom trawls were conducted successfully at 71 stations between Bering Strait and Pt. Barrow (Fig. 2). Station depth ranged from 12 to 90 m and the distance fished ranged from 0.5 to 1.5 km. All EBT bottom trawls were performed in accordance with standard NOAA trawling procedures (Stauffer 2004), see Goddard et al. (2014) for complete details. Biomass density (t km^{-2}) estimates were calculated using the area-swept method (Wakabayashi et al. 1985). The net-width was multiplied by the distance fished to determine the area trawled (km^{2}) for each haul. The weight of the catch for each species (t) was divided by the area trawled to determine the biomass density (t km^{-2}) at each station. The mean biomass density for the entire survey area was calculated as the sum of the station density estimates divided by the total number of stations sampled.

Catch data were also available from beam trawls that were conducted at 40 of the same sample stations during the 2012 trawl survey of the eastern Chukchi Sea. However, the EBT data was selected as the initial biomass inputs for the fish functional groups rather than the beam trawl data due to differences in sampling coverage and gear performance. We will briefly review the key differences in gear performance here as it relates to the selection of the EBT as our starting fish biomass estimates, but see Britt et al. (2013) for a more complete discussion and comparison of catch data from the two gear types.

In terms of gear performance, the four key differences between these two gears are area-swept, tow speed, vertical opening, and mesh size (Britt et al. 2013). The total area swept by the EBT is much larger than the area-swept by the beam trawl. This is due to a combination of factors: trawls with the EBT are of longer duration (15 min) than with the beam trawl (2-5 min), the EBT is towed at a higher speed (3 knots) than the beam trawl (1.5 knots), and the EBT is a much larger net than the beam trawl (see Britt et al. 2013 for the complete dimensions of both nets). The average area-swept by the EBT during a single haul was greater than the total area-swept by all 40 successful beam trawls combined during the 2012 survey (Britt et al. 2013). Bottom trawls were successfully completed with the EBT at 71 sampling stations and at 40 stations with the beam trawl. Overall, the total number of stations sampled and the total area-swept was far greater for the EBT than for the beam trawl.

After considering all the differences in gear design, performance, number of stations sampled, and total area-swept, we felt the EBT gave us the best overall estimates of fish biomass and therefore selected the EBT catch data as our initial biomass inputs for the fish groups. However, we note that the beam trawl may be more efficient at catching smaller and more slender fishes (Britt et al. 2013).

Production (P/B) and consumption (Q/B)

Under the assumption of steady-state conditions, P/B can be approximated by Z, the instantaneous mortality rate (Allen 1971). Following this relationship we use the regression estimator of the instantaneous natural mortality rate (M) developed by Hewitt and Hoenig (2005) as a proxy for the P/B of fish groups. This method requires a minimum amount of information, just an estimate of maximum age (t_{max}) from the stock in question.

Estimates of P/B and Q/B have been updated for all 4 species of the family Gadidae; Arctic cod (*Boreogadus saida*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Gadus chalcogrammus*), and saffron cod (*Eleginus gracilus*). We acquired estimates of maximum age for Arctic cod and saffron cod from Helser et al. (In press). The specimens used in Helser et al. (In press) were collected during Arctic Eis trawl surveys; the same trawl surveys from which the data used for initial biomass estimates were calculated, and were collected concurrent with the fish specimens collected for diet analysis (Whitehouse et al. In press).

The Q/B of fishes was calculated following the methods of Aydin (2004). This method requires an estimate of Z, the instantaneous mortality rate, and the von Bertalanffy growth parameter *k*. Estimates of the instantaneous mortality rate for Arctic cod and saffron cod were acquired from the previous calculation of P/B using the regression estimator of M developed by Hewitt and Hoenig (2005). Estimates of the von Bertalanffy *K* parameter for Arctic cod and saffron cod were acquired from Helser et al. (In press).

Region-specific data to support calculations of P/B and Q/B for walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*G. macrocephalus*) within the Chukchi Sea are not available. Maximum observed sizes for both walleye pollock and Pacific cod have generally been much smaller (<20 cm) in the Chukchi Sea (Wolotira et al. 1977, Barber et al. 1997, Norcross et al. 2010) than what is typically observed in the eastern Bering Sea. Therefore we did not feel it was appropriate to apply the P/Bs and Q/Bs previously calculated for the more southerly stocks found in the eastern Bering Sea (Aydin et al. 2007) to the corresponding groups in the Chukchi Sea model. Instead we apply the Chukchi Sea-specific estimates of P/B and Q/B for Arctic cod to walleye pollock and apply the Chukchi Sea-specific estimates for saffron cod to Pacific cod. Though there are many differences between Arctic cod and walleye pollock, both of these gadid species can be found occupying demersal and pelagic habitats, both feed on a variety of prey including zooplankton (Whitehouse et al. In press). Therefore, we felt the Chukchi Sea-specific P/B and Q/B were our best approximation of these parameters for walleye pollock. Similarly, during post-juvenile stages both saffron cod and Pacific cod are found primarily in the demersal environment and both feed predominantly on benthic and demersal prey (Wolotira 1985, Lang et al. 2005, Whitehouse et al. In press). We made the assumption that in the absence of region-specific data for Pacific cod, the region-specific saffron cod P/B and Q/B were a best approximation of the Pacific cod parameters.

Food habits (DC)

Stomachs were collected from fish caught during the 2012 Arctic Eis surface and bottom trawl surveys of the eastern Chukchi Sea. A total of 2,073 stomachs were collected and analyzed from 39 species of fish (Table 4). The collected specimens were preserved in buffered 10% formalin at sea following capture, and prepared for transport back to the Food Habits Lab in Seattle at the NOAA Alaska Fisheries Science Center (AFSC). The total contents of each stomach were weighed to the nearest 0.00001 g, then the contents were sorted and identified to the lowest practical taxon. Each prey taxa was counted, weighed, and its appropriate life history code identified. The diet data is maintained in the Resource Ecology and Ecosystem Modeling Program's (REEM) Food Habits Database at the AFSC. The predator diet compositions were acquired by querying the REEM food habits database (a detailed description of the database can be found at http://www.afsc.noaa.gov/REFM/REEM/Data/Default.htm) with their Diet Analysis Tool (Lang 2004). The diet compositions were calculated as the mean percent weight of each prey item in the predator's total stomach contents.

Nearly all prey items were assigned to existing model functional groups. However, some prey items could not be assigned to a model functional group (e.g., unidentified eggs, unidentified organic matter, etc.). These prey items, which seldom accounted for more than 1% (by weight) of a predator's total diet, were removed from the final diet. Because the Ecopath modeling framework requires predator diets to sum to one, these diets were renormalized to one after removal of the unidentified prey.

Table 4. -- Fish stomachs collected during Arctic Eis trawl surveys and analyzed to establish diet composition. Family totals are in bold and the same row as family name.

Family	Species name	Common name	Bottom trawl total	Off-bottom Chukchi total
Clupeidae (herrings)			**23**	**34**
	Clupea pallasi	Pacific herring	23	34
Osmeridae (smelts)			**41**	**134**
	Mallotus villosus	capelin	9	124
	Osmerus mordax	rainbow smelt	32	10
Gadidae (cods)			**812**	**82**
	Boreogadus saida	Arctic cod	714	82
	Eleginus gracilis	saffron cod	84	
	Gadus macrocephalus	Pacific cod	1	
	Gadus chalcogrammus	walleye pollock	13	
Hexagrammidae (greenlings)			**5**	
	Hexagrammos stelleri	whitespotted greenling	5	
Cottidae (sculpins)			**287**	
	Artediellus scaber	hamecon	22	
	Enophrys diceraus	antlered sculpin	20	
	Gymnocanthus tricuspis	Arctic staghorn sculpin	107	
	Hemilepidotus papilio	butterfly sculpin	1	
	Icelus spatula	spatulate sculpin	21	
	Myoxocephalus jaok	plain sculpin	1	
	Myoxocephalus quadricornis	fourhorn sculpin	2	
	Myoxocephalus scorpius	shorthorn (warty) sculpin	64	
	Triglops pingeli	ribbed sculpin	48	
Hemitripteridae (sailfin sculpins)			**10**	
	Nautichthys pribilovius	eyeshade sculpin	10	
Agonidae (poachers)			**52**	
	Podothecus veternus	veteran poacher	**5**	
	Ulcina olrikii	Arctic alligatorfish	47	
Liparidae (snailfishes)			**159**	
	Liparis gibbus	variegated snailfish	54	
	Liparis marmaratus	festive snailfish	7	
	Liparis tunicatus	kelp snailfish	98	
Zoarcidae (eelpouts)			**41**	
	Gymnelus hemifasciatus	halfbarred pout	1	
	Lycodes palearis	wattled eelpout	7	
	Lycodes polaris	Canadian eelpout	19	
	Lycodes raridens	marbled eelpout	10	
	Lycodes turneri	polar eelpout	2	
Stichaeidae (pricklebacks)			**175**	
	Lumpenus fabricii	slender eelblenny	148	
	Lumpenus medius	stout eelblenny	25	
	Stichaeus punctatus	Arctic shanny	2	
Ammodytidae (sand lances)			**5**	**53**
	Ammodytes hexapterus	Pacific sand lance	5	53
Pleuronectidae (flatfishes)			**163**	
	Hippoglossoides robustus	Bering flounder	114	
	Limanda aspera	yellowfin sole	13	
	Limanda proboscidea	longhead dab	7	
	Limanda sakhalinensis	Sakhalin sole	7	
	Liopsetta glacialis	Arctic flounder	13	
	Pleuronectes quadrituberculatus	Alaska plaice	8	
	Reinhardtius hippoglossoides	Greenland turbot	1	
Total stomachs collected for all families			**1770**	**303**
Grand total (bottom trawl and off-bottom collections)			**2073**	

New and changed fish functional groups

Three fish functional groups were added in this model update: the Alaska skate (*Bathyraja parmifera*), variegated snailfish (*Liparis gibbus*), and other snailfish (other than *L. gibbus*). Additionally, the species composition of the flatfish functional groups changed as Bering flounder (*Hippoglossoides robustus*) was removed from the small-mouth flatfish group and added to the large-mouth flatfish group.

Alaska skate

A single Alaska skate was caught in the south central Chukchi Sea during the 2012 bottom trawl survey of the eastern Chukchi Sea. This was the first live adult Alaska skate caught in the Chukchi Sea; previously, two beach cast specimens were found in 2010 near Pt. Hope and Kivalina (Mecklenburg et al. 2011). During the summer of 2010 several specimens of *B. parmifera* were caught in the northern Bering Sea during a NOAA bottom trawl survey (Lauth 2011, Stevenson and Lauth 2012). A steep increase in skate biomass (primarily *B. parmifera*) on the eastern Bering Sea continental shelf was observed between 1979 and 1990 and has remained steady since (Hoff 2006). Due to the observed increase of skate biomass in the eastern Bering Sea and the more recent records of Alaska skate in the northern Bering Sea and within the Chukchi Sea, we have added the Alaska skate to our eastern Chukchi Sea food web model as a single species functional group.

Variegated snailfish

In the original Ecopath model of the Chukchi Sea, the miscellaneous shallow fish functional group included poachers (Agonidae), wolffish (Anarhichadidae), lumpsuckers (Cyclopteridae), greenlings (Hexagrammidae), snailfish (Liparidae), and pricklebacks (Stichaeidae). In this updated model we have removed the variegated snailfish from the miscellaneous shallow fish functional group and it now forms its own single species functional group. The analysis of variegated snailfish stomachs collected during the 2012 eastern Chukchi Sea bottom trawl survey indicated that ~33% of their diet (by weight) consisted of other miscellaneous shallow fish. Approximately 13% of their diet was other liparids (*Liparis* sp.). To avoid the computational problems associated with functional group cannibalism, the variegated snailfish is now treated as a single species and not part of the larger miscellaneous shallow fish functional group.

Other snailfish

The third new fish functional group is snailfish, which includes all snailfish other than *L. gibbus*. These other snailfish species were formerly a part of the miscellaneous shallow fish functional group but were removed from it based on dietary differences. Approximately 18% of the snailfish diet consisted of fish, whereas none of the other species within the miscellaneous shallow fish group, for whom diet data was available, included any piscivory. Additionally, many of the non-snailfish species of the misc. shallow fish group were common prey items (especially stichaeids) in the diet of other piscivorous fishes. As the biomass estimate of the miscellaneous shallow fish group was top-down forced, their biomass increased commensurate with demand from predators. This had the effect of artificially increasing the biomass of the liparids because they were included in the same functional group with popular fish prey (e.g., stichaeids). As a result, the consumption of other fish by Liparids was also artificially increased. This looping of predator and prey ultimately resulted in inflated biomass levels for many of the fish functional groups, as most were top-down forced. The clear dietary distinctions between liparids and the rest of the miscellaneous shallow fish, in combination with the implications for top-down balancing of most fish functional groups, led us to the decision to separate snailfish from miscellaneous shallow fish into their own functional group.

Large-mouth flatfish and small-mouth flatfish

Bering flounder (*Hippoglossoides robustus*) was formerly included in the small-mouth flatfish group, along with yellowfin sole (*Limanda aspera*), longhead dab (*L. proboscidea*), Sakhalin sole (*L. sakhalinensis*), Arctic flounder (*Liopsetta glacialis*), starry flounder (*Platichthys stellatus*), and Alaska plaice (*Pleuronectes quadrituberculatus*), due to presumed similarities in diet and habitat requirements. Examination of the fish stomachs collected during the 2012 Arctic Eis surveys revealed that Bering flounders may be the only species in the small-mouth flatfish group that regularly preys on fish. We found that more than 50% of the Bering flounder diet composition (by weight) could be attributed to fish, while none of the stomachs collected for the other small-mouth flatfish species contained any fish prey. Due to this distinct difference in food habits we decided to remove Bering flounder from small-mouth flatfish and add them to large-mouth flatfish, which already includes two predators known to consume fish, Greenland turbot (*Rheinhardtius hippoglossoides,* also known as Greenland halibut) and Pacific halibut (*Hippoglossus stenolepis*).

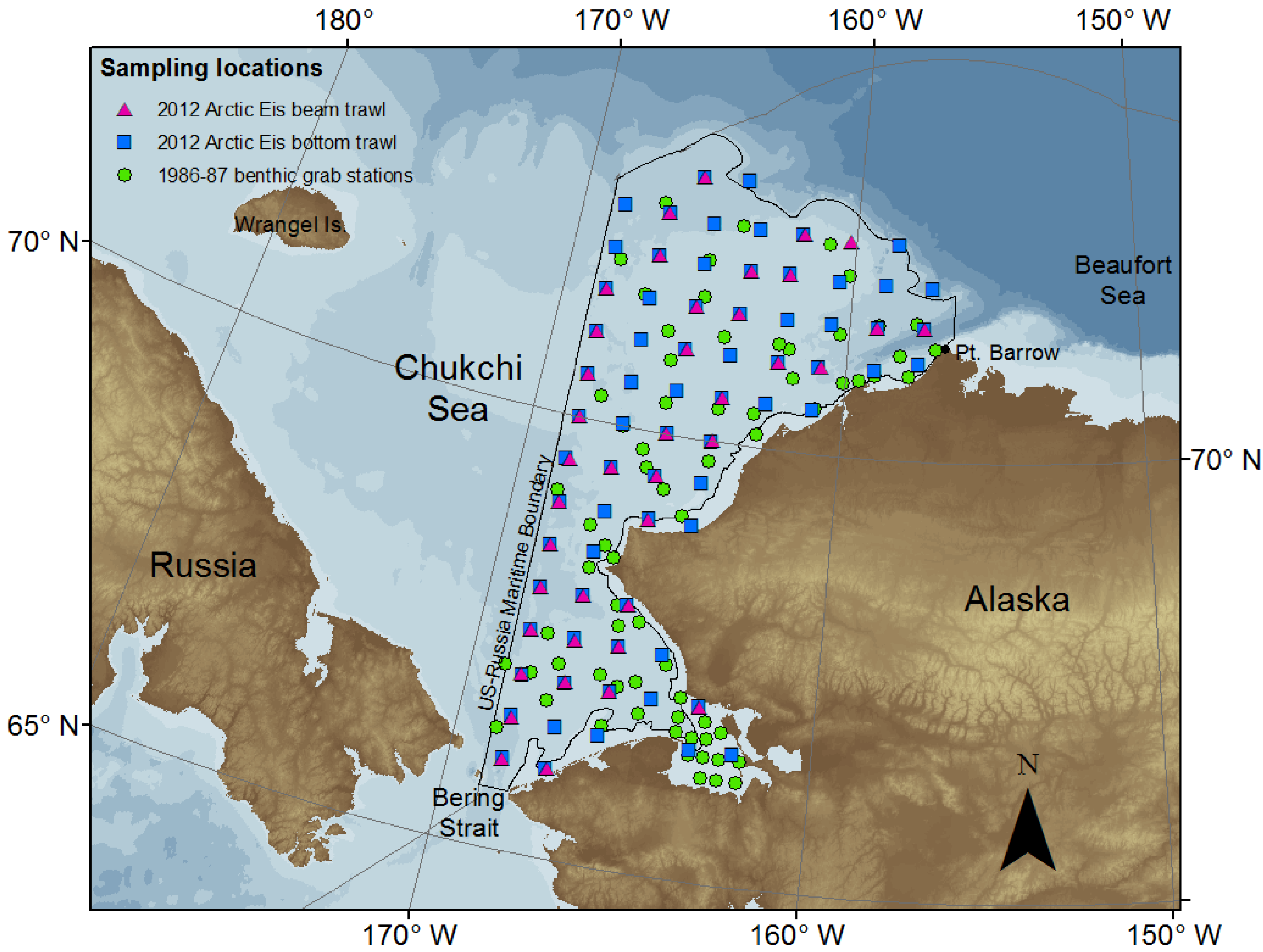

Figure 2. -- The sampling locations for the 2012 Arctic Eis bottom trawl and beam trawl stations (Britt et al. 2013). Arctic Eis bottom trawl stations are based on a 30 nautical mile (nmi) square grid pattern, with trawling locations at the center of each grid cell (Goddard et al. 2014). Also shown are the locations of benthic van Veen grab stations (Feder et al. 1994b, Feder et al. 2007).

Benthic Invertebrates

Biomass (B)

Biomass density (t km^{-2}) estimates for benthic invertebrates were derived from two principal sources: beam trawls and benthic grab samples. For the larger epifaunal invertebrates, biomass estimates were calculated from the catch data of beam trawls conducted during the 2012 Arctic Eis trawl survey of the eastern Chukchi Sea. For smaller benthic invertebrates that are poorly sampled by trawls, biomass estimates were calculated from benthic grab samples collected throughout the eastern Chukchi Sea in the mid-1980s (Feder et al. 1994b, Feder et al. 2007). Recent studies have examined the benthic infauna of the northeastern Chukchi Sea (Schonberg et al. (2014) for COMIDA-CAB and Blanchard et al. (2013b) for CSESP) but are not included here as they only cover a limited portion of our study area. Combining benthic grab data from the more recent studies with the grab data collected during the 1980s was deemed unacceptable as the data sets are separated by 23 or more years and inclusion of the recent studies would introduce a spatial bias towards the northeastern Chukchi Sea.

The beam trawls were conducted during August and September of 2012 aboard the chartered fishing vessel Alaska Knight. Beam trawls were conducted at a selected number of stations where bottom trawls were also performed (see Britt et al. (2013) for complete details). Beam trawls were successfully performed at 40 stations between 66°N and 73°N in the eastern Chukchi Sea (Figure 2). The trawls were performed with a plumb staff beam trawl with a 5.1 m footrope, 4.1 m headrope and a 4 mm codend liner. The effective net width is 2.3 m and the fishing scope was approximately 3.5:1 (Norcross et al. 2010). The trawling speed was about 1.5 knots and trawl duration was approximately 5 minutes. The plumb staff beam trawl is designed to maintain consistent contact with the bottom along the entire length of the footrope and is effective at catching benthic fauna, including individuals that make shallow burrows (Gunderson and Ellis 1986). Biomass density (t km^{-2}) estimates were calculated using the area-swept method (Wakabayashi et al. 1985). The net width was multiplied by the distance fished to determine the area trawled (km^2) for each haul. The weight of the catch for each species (t) was divided by the area trawled to determine the biomass density (t km^{-2}) at each station. The mean biomass density for the entire survey area was calculated as the sum of the station density estimates divided by the total number of stations sampled.

Quantitative benthic grab samples were collected with van Veen grabs (0.1 m^{-2}) at a total of 71 sampling stations across the eastern Chukchi Sea in 1986 and 1987 (Feder et al. 1994b, Feder et al. 2007). Two of the stations were excluded from our analysis due to incomplete data recording. Functional group density estimates (t km^{-2}) were averaged across all 69 sample stations (Figure 2).

Production (P/B) and Consumption (Q/B)

Estimates of P/B for benthic invertebrate groups that are both species-specific and specific to the Chukchi Sea are unavailable at this time. In the previous model, P/B estimates for related species from other regions or P/B estimates for taxonomically similar groups from other Ecopath models, were used in their place. These alternative P/B estimates were generally from studies conducted at lower latitudes, often in near shore (< 20 m depth) and intertidal waters. We updated the P/B estimates for many of the benthic invertebrates where improved estimates could be found in the literature. Estimates could be improved with greater geographic relevance (Arctic versus non-Arctic, data pedigree = 5), taxonomic relevance (e.g., same species different region, data pedigree = 5), or with estimates based on empirical methods (e.g., Cusson and Bourget 2005, data pedigree=6).

Input parameter estimates for Q/B and GE for benthic invertebrate functional groups remain unchanged from W13 . For several benthic invertebrate functional groups, reasonable estimates of Q/B are unavailable, and instead Q/B is calculated by Ecopath with an assumed GE of 0.2. GE usually ranges between 0.1 and 0.3 (Trites et al. 1999), and averages about 0.2 for benthic invertebrate groups in the eastern Bering Sea (Aydin et al. 2007). GE is calculated for most functional groups as P/B divided by Q/B. When a reasonable estimate of Q/B is unavailable, Q/B can be solved for by inserting an assumed GE value into the model. For those functional groups with updated P/B estimates and additionally have Q/B solved for with an assumed GE, Q/B is also be updated.

Food Habits (DC)

The diet compositions for benthic invertebrate functional groups remain unchanged from the preliminary model with the exception of snails. The diet composition of snails was updated with more specific diet data from the literature.

Unassimilated/consumption

The default value for the unassimilated fraction of consumption for carnivorous functional groups is 0.2. Unassimilated food is egested or excreted as feces and urine, and is directed to detritus. For herbivores and detritivores the unassimilated fraction is assumed to be higher and a default value of 0.4 is used.

Model Comparisons

We highlight similarities and differences between the preliminary model and our updated model by comparing the biomass of aggregated functional groups, and with a selection of ecosystem-scale metrics, including, total energy flow, total production, and total biomass (excluding detritus).

We examined how biomass is distributed across broad taxonomic categories by contrasting the biomass of aggregated groups between the preliminary model and the updated model. For this set of comparisons we aggregate together related functional groups into eight aggregate groups, and calculate an aggregated biomass by summing the biomass estimates for member groups. The eight aggregated groups are mammals, seabirds, fish, benthic invertebrates, jellyfish, zooplankton, microbes, and phytoplankton.

Total energy flow was measured as total system throughput (TST), which is the sum of total mass flows (t km^{-2} $year^{-1}$) for consumption, respiration, flow to detritus, and export (Christensen et al. 2005). Total consumption is the sum of food intake (B*Q/B) by all predators. Respiration flow is the fraction of assimilated food that does not lead to production. The flow to detritus from each group is a combination of the unassimilated portion of food that egested and the portion of the group that is lost to other sources of mortality outside of the predation and fisheries mortality explicitly included in the model. We looked at the magnitude and direction of change in TST from the preliminary model to this model update.

Total ecosystem production is the sum of production (t km^{-2} $year^{-1}$) from all functional groups. Similarly, total biomass is the sum of biomass estimates (t km^{-2}) for all living groups. We examined how total production and total biomass have changed from the preliminary model to this model update and discussed possible explanations for those changes. Additionally, we calculate the ratio of total system production to total biomass (P/B). Whitehouse et al. (2014) also calculated the ratio of total ecosystem production to total biomass for the preliminary model and interpreted it as an overall measure of ecosystem turnover.

RESULTS

Outline

Here we present descriptions of new input parameters and the output parameters that result from balancing the updated model (e.g., top-down balanced biomass). The results section is organized as follows. First, we present results of the updated model for each functional group, in turn. For each functional group we note which basic input parameters (B, P/B, Q/B, DC, and C) were updated with new information and those parameters that remain unchanged from the preliminary model. For updated parameters we provide a detailed description of parameter development and data sources. An updated data pedigree can be found in Appendix B. For those model parameters that are not updated and remain unchanged from the preliminary model, they are not discussed at length here and instead the reader is directed to the preliminary model documentation (i.e., W13, Whitehouse et al. 2014). However, for those parameters not updated in this report we do include the parameter values and the core references informing those parameter estimates. Second, in the Model Balancing section we summarize the key adjustments to the model structure and input parameters that were made during the model balancing process. These are adjustments that were made after all input parameters were selected, but were necessary to bring the model into balance. Last, we present results for the ecosystem as a whole, in the Model Comparison section. There we present a collection of ecosystem scale metrics and compare these results with similar metrics calculated for the preliminary model.

Cetaceans

Beluga

Belugas (*Delphinapterus leucas*) are toothed whales (Odontoceti) from the family Monodontidae. Two stocks of belugas (*Delphinapterus leucas*) occur in the Chukchi Sea, the Chukchi Sea stock and the Beaufort Sea stock. Both stocks overwinter in the Bering Sea and migrate north through the Bering Strait and into the Chukchi Sea in spring when the sea ice begins to fracture (Frost et al. 1983, Moore et al. 1993).

Updated parameters

None

Parameters from W13

The beluga biomass estimate (B) is based on population estimates for the eastern Chukchi Sea stock and the Beaufort Sea stock taken from Allen and Angliss (2010). The abundance estimate is multiplied by a mean adult beluga body mass from Hunt et al. (2000), then reduced to reflect seasonal occupancy of the model area and migration patterns, resulting in a biomass estimate of 0.01159 t km^{-2}. P/B was estimated to be 0.11 using a variant of Siler's competing risk model (Siler 1979), as modified by Barlow and Boveng (1991). A Q/B of 14.50 was estimated from daily caloric requirements scaled up to an annual rate and calculated following the methods of Perez et al. (1990). The diet composition (DC) of belugas is estimated to include primarily fish (~90%) and secondarily cephalopods and shrimp (~10%) (Seaman et al. 1982). The beluga subsistence harvest (C) is estimated as $6.34 * 10^{-5}$ t km^{-2} based on information in Allen and Angliss (2010).

Gray whale

Gray whales (*Eschrichtius robustus*) are baleen whales (Mysteceti) that spend the winters in Baja California and migrate north to the northern Bering and Chukchi seas during summer (Braham 1984) where they feed on the abundant communities of benthic invertebrates (Highsmith and Coyle 1990, Highsmith et al. 2006).

Updated parameters

Biomass (B): Updated gray whale biomass is calculated from an abundance estimate of 19,126 whales, corresponding to the years 2006-07 (Laake et al. 2009). This abundance estimate was reduced by half to account for seasonal occupation of the model area. It was reduced further to account for the fraction of whales migrating into the Chukchi Sea (~0.7) (Highsmith and Coyle 1992), and to account for the estimated proportion occupying the eastern Chukchi Sea (0.333). The remaining abundance estimate is multiplied by an average body mass of 16,177 kg (Hunt et al. 2000) then divided by the total model area (192,054 km^{-2}) to arrive at a gray whale model biomass of 0.188 t km^{-2}.

Parameters from W13

The P/B of 0.06 for gray whales was previously estimated by Aydin et al. (2007) using a variant of Siler's competing risk model (Siler 1979), as modified by Barlow and Boveng (1991). A Q/B of 8.87 was calculated by scaling the daily requirements listed in Hunt et al. (2000) up to an annual rate. The diet (DC) of gray whales primarily consists of benthic invertebrates, and is particularly dominated by benthic amphipods (Nerini 1984, Highsmith and Coyle 1990, 1992). Their diet is estimated to consist of 90% benthic amphipods with the remaining 10% divided among other benthic invertebrate prey.

Bowhead whale

Bowhead whales (*Balaena mysticetus*) are baleen whales that migrate through the Chukchi Sea on their way between the northern Bering Sea where they spend the winter, and the Beaufort Sea where they spend the summer.

Updated parameters

Biomass (B): Updated bowhead whale biomass is based on the most recent abundance estimate of 12,631, describing the population in 2004 (Koski et al. 2010). Biomass was calculated following the same methods as W13, using a mean body mass of 31,056 kg (Hunt et al. 2000) and accounting for seasonal use of the model area. The resulting bowhead biomass density in the model is 0.398 t km^{-2}.

Subsistence harvest (C): Bowhead whales are taken in subsistence harvests by Natives of Alaska, Russia, and Canada. Most recently, the annual average Native harvest over the years 2006 to 2010 was 38 whales (Allen and Angliss 2013). We use this estimated annual average harvest as a best estimate of bowhead whale harvest (C = 0.00120 t km^{-2}).

Parameters from W13

The bowhead whale P/B of 0.01 was derived by Aydin et al. (2007) from survival estimates reported in Zeh et al. (2002). Q/B was estimated to be 5.26 by scaling the daily caloric requirements for bowheads listed in Hunt et al. (2000) up to an annual rate. Bowhead whales primarily consume pelagic invertebrates but small amounts of benthic invertebrates have also been recorded in stomach contents (Lowry and Burns 1980, Hazard and Lowry 1984, Lowry 1993, Moore et al. 2010). Their DC is estimated as 71% copepods, 24% other zooplankton, and 5% benthic invertebrates including other crabs, benthic amphipods, and other epifauna and infauna.

Caniforms

Polar bear (Chukchi stock)

There are two stocks of polar bears (*Ursus maritimus*) found in Alaska, the Chukchi/Bering stock and the southern Beaufort Sea stock (USFWS 2010a, b). The distributions of the two stocks overlap with bears from the Chukchi stock found east of Pt. Barrow and bears from the southern Beaufort Sea stock found as far west as Icy Cape along the Chukchi Sea coast (Amstrup et al. 2005).

Updated parameters

None

Parameters from W13

The biomass (B) of the Chukchi stock of polar bears is based on the best available population estimate of 2,000 bears, which is a revised estimate of this population based on an extrapolation of denning data from Wrangel Island (Lunn et al. 2002, Aars et al. 2006, Obbard et al. 2010, USFWS 2010a). The estimate was reduced to reflect occupancy of the model area and account for seasonal loss of sea ice and patterns in bear movement (Garner et al. 1990, Garner et al. 1994, Amstrup et al. 2005). The reduced abundance estimate was then multiplied by an average individual body mass (310 kg) derived from Derocher (1991), then divided by the model area to arrive at an estimated density of $4.04 * 10^{-4}$ t km^{-2}. The P/B of the Chukchi stock is estimated to be 0.06, which is based on an estimated annual intrinsic growth rate for the southern Beaufort Sea stock (Amstrup 1995) but is recommended as a best estimate for the Chukchi stock (USFWS 2010a). The Q/B of polar bears was calculated using information on the estimated polar bear basal metabolic rate (Best 1977) and daily metabolic rate (Best 1985), along with the estimated caloric density of their primary prey, ringed seals (*Phoca hispida*) (Stirling and McEwan 1975). When scaled up to an annual rate, this resulted in an estimated P/B of 4.00. The primary prey of polar bears, throughout their range, is ringed seals, and of secondary importance are bearded seals (*Erignathus barbatus*) (Stirling and Archibald 1977, Smith 1980, Derocher et al. 2002, Iverson et al. 2006, Bentzen et al. 2007). They are also known to consume belugas (Freeman 1973, Smith 1985, Lowry et al. 1987, Smith and Sjare 1990, Rugh and Shelden 1993), walrus (Kiliaan and Stirling 1978, Amstrup and DeMaster 1988, Calvert and Stirling 1990), and to opportunistically feed on whale carcasses either from subsistence hunts or beached whales (Kochnev 2006, Miller et al. 2006, Ovsyanikov 2010). The diet composition (DC) used here for both stocks of polar bears was derived through fatty acid analysis by Thiemann et al. (2008) and consists of approximately 65% ringed seal, 25% bearded seal, and 10% beluga. Polar bears from the Chukchi stock may be harvested for subsistence purposes or killed due to human interactions in both the United States and Russian portions of their range (Belikov 1995, DeBruyn et al. 2010, USFWS 2010a). The harvest of polar bears (C) was estimated from values reported in Schliebe and Evans (1995) and Belikov (1995) for a combined U.S. and Russian harvest of $1.61 * 10^{-5}$ t km^{-2}.

Polar bear (Southern Beaufort stock)

There are two stocks of polar bears (*Ursus maritimus*) found in Alaska, the Chukchi/Bering stock and the southern Beaufort Sea stock (USFWS 2010a, b). Bears from the southern Beaufort Sea stock regularly occur in the Chukchi Sea and are found as far west as Icy Cape along the Chukchi Sea coast (Amstrup et al. 2005).

Updated parameters

None

Parameters from W13

The estimated biomass **(B)** for the southern Beaufort stock of polar bears is based on an abundance estimate of 1,526 in the years 2004-2006 (Regehr et al. 2006). This abundance estimate was reduced to represent the time spent in the model area and polar bear movement patterns (Amstrup 1995, Amstrup et al. 2005). The reduced abundance estimate was then multiplied by an average individual body mass (310 kg) derived from Derocher (1991), then divided by the model area to arrive at an estimated density of $1.2 * 10^{-4}$ t km^{-2}. The estimated P/B of 0.06 for the southern Beaufort stock of polar bears is based on an estimated annual intrinsic growth rate of 6.03% for this stock (Amstrup 1995). The Q/B of the southern Beaufort stock of polar bears was calculated exactly the same as for the Chukchi stock; using information on the estimated polar bear basal metabolic rate (Best 1977) and daily metabolic rate (Best 1985), along with the estimated caloric density of their primary prey, ringed seals (*Phoca hispida*) (Stirling and McEwan 1975). When scaled up to an annual rate, this resulted in an estimated Q/B of 4.00. The diet composition (DC) used for the southern Beaufort Sea stock of polar bears is exactly the same as the diet assumed for the Chukchi Sea stock of polar bears. We use the diet composition derived through fatty acid analysis by Thiemann et al. (2008) which includes 65% ringed seal, 25% bearded seal, and 10% beluga. Polar bears from the southern Beaufort Sea stock may be harvested for subsistence purposes or killed due to human interactions (DeBruyn et al. 2010, USFWS 2010b). The subsistence harvest (C) of polar bears from this stock was estimated to be $2.26 * 10^{-6}$ t km^{-2} from values reported in Schliebe and Evans (1995).

Pacific walrus

The Pacific walrus (*Odobenus rosmarus divergens*) is the largest pinniped in the Alaska Arctic and is easily recognized by its prominent large tusks. They overwinter in the northern Bering Sea and migrate north into the Chukchi Sea during spring, following the receding ice-edge (Fay 1982).

Updated parameters

Biomass (B): We updated the Pacific walrus biomass estimate based on the most recent abundance estimate of 129,000 for 2006 (Speckman et al. 2011). The new biomass estimate was calculated following the methods of W13, accounting for seasonal occupation of the model area, and spatial distribution outside of the model area. Using body mass estimates from Trites and Pauly (1998), this resulted in a Pacific walrus model biomass density of 0.059 t km^{-2}.

Parameters from W13

A P/B of 0.07 was estimated for Pacific walrus using a variant of Siler's competing risk model (Siler 1979), as modified by Barlow and Boveng (1991). The Q/B of Pacific walrus was estimated using the prey caloric density and daily caloric requirements reported in Hunt et al. (2000). Scaling up to an annual rate resulted in a Q/B of 21.66. The primary prey of Pacific walrus throughout their range are bivalves but the exact composition of their diet varies with season and location (Fay 1982, Fay et al. 1986, Dehn et al. 2007, Sheffield and Grebmeier 2009). The estimated diet composition (DC) for Pacific walrus in the preliminary model is based on the generalized diet described by Perez (1990) and is dominated by bivalves (69.9%). Prey groups of lesser importance include sea cucumbers, anemones, tunicates, marine worms, benthic amphipods, crabs, snails, shrimp, and octopus. The subsistence harvest (C) is based on the average of harvest of 6,713 walrus by both the U.S. and Russia over the years 1960-2007 (USFWS 2010c)

Bearded seal

The Bering-Chukchi seas stock of bearded seals (*Erignathus barbatus*) are found throughout the continental shelf waters (< 200 m depth) of the Pacific Arctic, including the Bering, Chukchi, East Siberian, and Beaufort seas (Cameron et al. 2010). Bearded seals are benthic foragers and the seasonal ice coverage, shallow depths, and large area of the continental shelf in the Pacific Arctic provides a large continuous expanse of habitat suitable for bearded seals (Burns and Frost 1983).

Updated parameters

Food habits (DC): Bearded seals are benthic foragers with flexible diets that typically include brachyuran crabs, shrimp, mollusks, and fish (Kenyon 1962, Johnson et al. 1966, Lowry et al. 1980a, Lowry et al.

1983, Dehn et al. 2007). The bearded seal diet in the preliminary model was derived from food habits data reported in Lowry et al. (1980a) for bearded seals collected in the Chukchi Sea. The dominant prey groups are bivalves (33%), shrimp (25%), and snow crab (19.5%). The bearded seal diet from the preliminary model has been updated here reflecting the move of Bering flounder from the small-mouth flatfish group to the large-mouth flatfish group. Flatfish have been previously noted as prey to bearded seals (Lowry et al. 1980a, Burns and Frost 1983, Lowry et al. 1983, Antonelis et al. 1994), however species-level identifications of flatfish prey are not available. Antonelis et al. (1994) were able to identify *Hippoglossoides* sp. among the stomach contents of bearded seals collected near St. Matthew Island in the eastern Bering Sea. In the preliminary model small-mouth flatfish were the only flatfish included in the bearded seal diet. Lacking guidance on how to accurately attribute the flatfish portion of the bearded seal diet, in this model update we have divided this part of the diet evenly between both flatfish groups (2.1% each).

Parameters from W13

The biomass (B) of bearded seals within the model was estimated to be 0.03905 t km^{-2} based on an average individual body mass from Trites and Pauly (1998); limited available information on population abundance from Burns (1981b), Cameron et al. (2010), and Ver Hoef et al. (2013); and uncertain information on migration patterns (Burns 1981b, Burns and Frost 1983). The P/B estimate of 0.08 was calculated with a generalized model for marine mammal survivorship (Barlow and Boveng 1991). The bearded seal Q/B of 12.94 was calculated with estimates of prey caloric density from Hunt et al. (2000) and daily caloric requirements calculated following the methods of Perez et al. (1990). The estimated subsistence harvest (C) of 0.00177 t km^{-2} was derived from annual harvest estimates from Allen and Angliss (2011).

Ringed seal

Ringed seals (*Phoca hispida*) are found throughout the Arctic including the Bering, Chukchi, and Beaufort seas in Alaska (Kelly et al. 2010). They are year-round residents in ice-covered Arctic waters and are able to maintain breathing holes in the ice by scratching the ice with claws on their foreflippers (Johnson et al. 1966, Lowry et al. 1983, Kelly 1988).

Updated parameters

None

Parameters from W13

The biomass estimate (B) of 0.05587 t km^{-2} for ringed seals is derived from abundance estimates in Bengtson et al. (2005), and estimates of average individual body mass from Trites and Pauly (1998). The estimated P/B of 0.09 for ringed seals was calculated with the generalized model for marine mammal survivorship from Barlow and Boveng (1991). The ringed seal Q/B of 19.23 was calculated with estimates of prey caloric density from Hunt et al. (2000) and daily caloric requirements calculated following the methods of Perez et al. (1990). Ringed seals have a diverse diet that includes both fishes and crustaceans. Arctic cod and saffron cod are the dominant fish prey, and shrimp are the dominant crustacean prey of ringed seals (Lowry et al. 1980b, Lowry et al. 1983). The diet composition (DC) used here is from Perez (1990), who compiled diet information for ringed seals from multiple studies in the eastern Chukchi, Beaufort, and northern Bering seas. The three most dominant prey types are Arctic cod (45%), saffron cod (33%), and shrimp (10%). The model harvest estimate (C) of 0.00212 t km^{-2} is based on estimated annual Alaska harvest from Allen and Angliss (2011).

Spotted seal

In Alaska, the range of spotted seals includes the Chukchi, Bering, and Beaufort seas. They spend the winter in the Bering Sea near the southern edge of the ice pack among smaller ice floes, and migrate north and coastward into the northern Bering, Chukchi, and Beaufort seas during spring and summer when the sea ice breaks up (Burns 1970, Frost et al. 1983, Braham et al. 1984, Lowry et al. 2000, Simpkins et al. 2003).

Updated parameters

Food habits (DC): The diet of spotted seals in the eastern Chukchi Sea and Bering Sea is dominated by fish, including Arctic cod, saffron cod, and pelagic forage fish (Lowry et al. 1983, Bukhtiyarov et al. 1984, Dehn et al. 2007). The diet composition used in W13 was based on the spotted seal diet composition presented in Perez (1990), which was compiled from multiple studies conducted throughout the species range in the Bering and Chukchi seas. The primary prey items in the spotted seal diet are pelagic forage fish (46%), Arctic cod (22%), large-mouth sculpins (12%), and saffron cod (9%). We have updated the spotted seal diet composition to reflect the move of Bering flounder from the small-mouth flatfish group to large-mouth flatfish. Previous diet studies have indicated flatfish are prey for spotted seals (Lowry et al. 1983, Bukhtiyarov et al. 1984, Dehn et al. 2007); however, species-level identifications of flatfish prey are unavailable. In the absence of species-level guidance to properly attribute the flatfish portion of their diet, we have divided this part of their diet evenly between the two flatfish functional groups (0.85% each).

Parameters from W13

The spotted seal biomass estimate (B) of 0.00579 t km^{-2} was based on information from stock assessments (Allen and Angliss 2013), multiple studies on population abundance (Burns 1986, Reeves et al. 1992, Boveng et al. 2009, Ver Hoef et al. 2013), and information on migration patterns (Frost et al. 1993). The estimated average individual body mass was derived from information in Trites and Pauly (1998). The spotted seal P/B of 0.07 was estimated from a general model for marine mammal survivorship (Barlow and Boveng 1991). The spotted seal Q/B of 18.70 was calculated with estimates of prey caloric density from Hunt et al. (2000) and daily caloric requirements calculated following the methods of Perez et al. (1990). The modeled spotted seal subsistence harvest (C) of $1.52*10^{-4}$ t km^{-2} was based on an estimated annual harvest of 5,265 seals (Allen and Angliss 2011).

Seabirds

All seabirds

Biomass (B)

We calculated biomass estimates for 20 species of seabirds known to occupy the eastern Chukchi Sea (plus unidentified murres [*Uria* sp.]). The biomass estimates for Procellarids and Scolopacids are based on population estimates from Divoky (1987) and the biomass estimates for Cormorants, Larids, Alcids piscivorous, and Alcids planktivorous are based on colony counts from the Seabird Information Network (2011) (Table 5).

Production (P/B)

We calculated estimates of P/B for all seabird functional groups (Table 6) based on adult survival rates (Schreiber and Burger 2001). The functional group P/Bs are average P/Bs weighted by the biomass of the functional group's species.

Consumption (Q/B)

Estimates of Q/B were calculated for all seabird functional groups based on average individual body mass, mean energy density of prey, and estimated daily energy requirements (Table 7). The Q/B of a seabird functional group is an average of the constituent species Q/Bs weighted by biomass.

Table 5. -- Biomass estimates for seabird functional groups. *Colony counts are from the Seabird Information Network (2011), and †Population estimates are from Divoky (1987). Estimates of mean individual body mass are from Hunt et al. (2000). ΩDensity is calculated as either the colony count or population estimate multiplied by 1/3 to account for seasonal occupation, then divided by the total model area, 192,054 km^2.

Functional Group	Common name	Species	*colony count	†pop. Est.	Ωdensity (birds km^{-2})	mean body mass (t)	B (t km^{-2})	Group B (t km^{-2})
Procellarids								0.001927375
	Northern fulmar	*Fulmaris glacialis*		45,000	0.078103	0.000544	4.24881E-05	
	Short-tailed shearwater	*Puffinus tenuirostris*		2,000,000	3.471246	0.000543	0.001884887	
Cormorants								
	Pelagic cormorant	*Phalacrocorax pelagicus*	453		0.000786	0.001868	1.46869E-06	1.46869E-06
Scolopacids				1,000,000	1.735623	0.00004475	7.76691E-05	7.76691E-05
	Red-necked phalarope	*Phalaropus lobatus*				0.0000338		
	Red phalarope	*P. fulicarius*				0.0000557		
Larids								9.31276E-05
	Mew gull	*Larus canus*	20		0.000035	0.0004035	1.40065E-08	
	Glaucous gull	*L. hyperboreus*	3,534		0.006134	0.0014125	8.66384E-06	
	Black-legged kittiwake	*Rissa tridactyla*	119,323		0.207100	0.000407	8.42896E-05	
	Aleutian tern	*Sterna aleutica*	393		0.000682	0.00012	8.1852E-08	
	Arctic tern	*S. paradisaea*	410		0.000712	0.00011	7.82766E-08	
Alcids piscivorous								0.001155027
	Common murre	*Uria aalge*	82,470		0.143137	0.0009925	0.000142063	
	Thick-billed murre	*U. lomvia*	152,330		0.264387	0.000964	0.000254869	
	Unidentified murre	*Uria* spp.	435,305		0.755525	0.0009742	0.000736033	
	Tufted puffin	*Fratercula cirrhata*	508		0.000882	0.000779	6.86842E-07	
	Horned puffin	*F. corniculata*	19,670		0.034140	0.000619	2.11325E-05	
	Pigeon guillemot	*Cepphus Columba*	109		0.000189	0.000487	9.21321E-08	
	Black guillemot	*C. grille*	225		0.000391	0.0003832	1.49645E-07	
Alcids planktivorous								0.000139496
	Crested auklet	*Aethia cristatella*	219,000		0.380101	0.000264	0.000100347	
	Parakeet auklet	*A. psittacula*	20,000		0.034712	0.000258	8.95581E-06	
	Least auklet	*A. pusilla*	207,000		0.359274	0.000084	3.0179E-05	
	Dovekie	*Alle alle*	50		0.000087	0.000163	1.41453E-08	

Table 6. -- Seabird functional group P/B estimates. Species-specific annual survival rates and order level adult survival rates are from Schreiber and Burger (2001). The functional group P/B is an average P/B weighted by the estimated biomass of the constituent species within the model area. Where annual survival rates were given as a range, we used the midpoint of that range in calculations.

Functional group	Common name	Species	Annual survival rate	Order level adult survival rate	S	P/B=-ln(S)	Group P/B
Procellarids							0.0667
	Northern fulmar	*Fulmaris glacialis*	0.94-0.97		0.955	0.0460	
	Short-tailed shearwater	*Puffinus tenuirostris*	0.93-0.94		0.935	0.0513	
Cormorants							0.1625
	Pelagic cormorant	*Phalacrocorax pelagicus*		0.85	0.85	0.1625	
Scolopacids							0.1625
	Red-necked phalarope	*Phalaropus lobatus*		0.85	0.85	0.1625	
	Red phalarope	*P. fulicarius*		0.85	0.85	0.1625	
Larids							0.1057
	Mew gull	*Larus canus*		0.85	0.85	0.1625	
	Glaucous gull	*L. hyperboreus*		0.85	0.85	0.1625	
	Black-legged kittiwake	*Rissa tridactyla*	0.88-0.93		0.905	0.0998	
	Aleutian tern	*Sterna aleutica*		0.85	0.85	0.1625	
	Arctic tern	*S. paradisaea*	0.90		0.90	0.1054	
Alcids piscivorous							0.1041
	Common murre	*Uria aalge*	0.87-0.95		0.91	0.0943	
	Thick-billed murre	*U. lomvia*	0.89-0.9		0.895	0.1109	
	Unidentified murre	*Uria* spp.			†0.90037	0.1050	
	Tufted puffin	*Fratercula cirrhata*	*0.942		0.942	0.0598	
	Horned puffin	*F. corniculata*	*0.942		0.942	0.0598	
	Pigeon guillemot	*Cepphus columba*	0.80		0.80	0.2231	
	Black guillemot	*C. grylle*	0.87		0.87	0.1393	
Alcids planktivorous							0.1404
	Crested auklet	*Aethia cristatella*	0.89		0.89	0.1165	
	Parakeet auklet	*A. psittacula*		0.85	0.85	0.1625	
	Least auklet	*A. pusilla*	0.808		0.808	0.2132	
	Dovekie	*Alle alle*		0.85	0.85	0.1625	

†Average survival rate of thick-billed and common murres, weighted by biomass.

* Annual survival rate for Atlantic puffin (*Fratercula arctica,* Schreiber and Burger 2001)

Table 7. -- Q/B values for seabird functional groups. Mean body mass and daily energy needs are taken from Hunt et al. (2000). Mean prey energy density calculated with approximate energy densities reported in Table 3, weighted by diet composition (see diet matrix or functional group accounts for diet composition). Functional group Q/B is the average Q/B of the constituent species, weighted by their estimated biomass in the model area.

Functional group	Common name	Species	Mean body mass (kg)	Daily energy needs (kj)	Mean prey energy density (kj/g)	Q/B	Functional group Q/B
Procellarids							187.928
	Northern fulmar	*Fulmaris glacialis*	0.544	1116.299	3.5	213.996	
	Short-tailed shearwater	*Puffinus tenuirostris*	0.543	1114.806	4	187.341	
Cormorants							142.618
	Pelagic cormorant	*Phalacrocorax pelagicus*	1.868	2737.102	3.75	142.618	
Scolopacids							374.313
	Red-necked phalarope	*Phalaropus lobatus*	0.0338	148.089	4	399.796	
	Red phalarope	*P. fulicarius*	0.0557	212.930	4	348.830	
Larids							205.674
	Mew gull	*Larus canus*	0.4035	898.356	4.155	195.560	
	Glaucous gull	*L. hyperboreus*	1.4125	2233.786	4.5	128.272	
	Black-legged kittiwake	*Rissa tridactyla*	0.407	904.014	3.798	213.437	
	Aleutian tern	*Sterna aleutica*	0.12	372.019	4.151	272.629	
	Arctic tern	*S. paradisaea*	0.11	349.215	3.36	344.868	
Alcids piscivorous							178.383
	Common murre	*Uria aalge*	0.9925	1728.316	3.686	172.433	
	Thick-billed murre	*U. lomvia*	0.964	1692.092	3.526	181.721	
	Unidentified murre	*Uria* spp.	*0.974	1705.090	3.583	178.295	
	Tufted puffin	*Fratercula cirrhata*	0.779	1449.265	4	169.763	
	Horned puffin	*F. corniculata*	0.619	1226.194	4	180.760	
	Pigeon guillemot	*Cepphus columba*	0.487	1029.991	3.863	199.859	
	Black guillemot	*C. grylle*	†0.3832	865.267	3.07	268.460	
Alcids planktivorous							247.507
	Crested auklet	*Aethia cristatella*	0.264	659.942	4	228.105	
	Parakeet auklet	*A. psittacula*	0.258	649.004	3.7	248.153	
	Least auklet	*A. pusilla*	0.084	287.046	4	311.820	
	Dovekie	*Alle alle*	0.163	464.794	4	260.199	

†Mean body mass calculated from values reported by Berzins et al. (2009).

*Mean individual body mass calculated as average of values reported for common murre and thick-billed murre, weighted by estimated biomass within the model area.

Procellarids

The Procellarid functional group is represented by two species, the northern fulmar (*Fulmaris glacialis*) and the short-tailed shearwater (*Puffinus tenuirostris*), which are the most abundant Procellarids found in the eastern Chukchi Sea during the ice-free season (Divoky 1987, Gall et al. 2013).

Updated parameters

Biomass (B): Density estimates for Procellarids were calculated from the coarse population abundance estimates reported by Divoky (1987). Divoky (1987) estimated there to be 45,000 northern fulmars and 2,000,000 short-tailed shearwaters at their peak abundance during the ice-free season. The abundance estimates were used in combination with estimates of average individual body mass from Hunt et al. (2000) to arrive at a group biomass of 0.0019 t km^{-2} (Table 5).

Production (P/B): The Procellarid P/B was calculated from species-specific annual survival rates (Table 6). The range of annual survival rates for northern fulmars is 0.94-0.97, and for short-tailed shearwaters it is 0.93-0.94. Using the midpoint of these survival rate ranges, we calculated a weighted (by biomass) group P/B of 0.067.

Consumption (Q/B): The Q/B for Procellarids was calculated assuming a mean body mass of 0.544 kg for northern fulmars and 0.543 kg for short-tailed shearwaters (Hunt et al. 2000). The Q/B for northern fulmars is 214 and 187 for short-tailed shearwaters. The functional group Q/B of 187.928 is an average Q/B weighted by the estimated biomass of the two species.

Food habits (DC): Northern fulmars feed on prey at the water's surface and are capable of shallow dives, up to 3 m depth (Hobson and Welch 1992). In the eastern Bering Sea they are found in close association with commercial fishing vessels and are known to feed on offal (Hunt et al. 1981). Their diet in the eastern Bering Sea includes walleye pollock (55%, *Gadus chalcogrammus*), cephalopods (25%), other fish (10%), amphipods (5%), and euphausiids (5%); though the amount of walleye pollock that can be attributed to fishery discards as opposed to wild caught prey is difficult to interpret due to the fulmars' known affinity for fishing vessels (Hunt et al. 1981). Phillips et al. (1999) reviewed the diet of northern fulmars at several high latitude locations and found their diet to generally consist of juvenile gadids, pelagic forage fish, and pelagic zooplankton. Birds from more southerly parts of their range had greater proportions of their diet attributed to fishery discards (Phillips et al. 1999). As there are no large scale commercial fisheries in the eastern Chukchi Sea, we assume there is no offal consumption by northern fulmars within our study area. In the Frans Josef Land archipelago (Russian Arctic), the dominant prey of northern fulmars by % weight were Arctic cod (50.7%) and *Myoxocephalus scorpius* (34.9%) (Weslawski et al. 1994). In the Canadian High Arctic, northern fulmars have been found to feed on fish (primarily Arctic cod), copepods, amphipods, other zooplankton, cephalopods, and polychaetes (Bradstreet and Cross 1982, Byers et al. 2010, Mallory et al. 2010). In pelagic waters of the marginal ice zone in eastern Svalbard, the most frequently encountered prey in northern fulmar stomachs were nereid polychaetes, squids, and Arctic cod (Mehlum and Gabrielsen 1993). In the northern Bering Sea, northern fulmars have been observed feeding in association with the mud plumes of benthic foraging gray whales, where they consumed primarily benthic amphipods (Obst and Hunt 1990, Grebmeier and Harrison 1992). Additionally, there are observations of northern fulmars opportunistically scavenging on marine mammal remains from subsistence hunts (Bradstreet 1982, Haney 1988, Hobson and Welch 1992, Mallory et al. 2010) but this does not appear to be an important part of the diet. Lacking region-specific data, and considering the available data, we are attributing 50% of the diet to Arctic cod, 20% to copepods, 20% to other zooplankton, and 10% to amphipods.

Short-tailed shearwaters forage for prey by seizing the prey at the water's surface, plunging or diving for prey underwater, hydroplaning, or opportunistically scavenging on floating remains (Ogi et al. 1980). Throughout the Bering Sea and north Pacific, their diet generally contains euphausiids, hyperiid amphipods, larval and juvenile fish, squid, and pteropods (Ogi et al. 1980, Hunt et al. 1981). In the eastern Bering Sea the most common fish prey species are walleye pollock, capelin, and Pacific sand lance (Ogi et al. 1980, Hunt et al. 1981, Hunt et al. 2002). Ogi et al. (1980) separately examined the diet of short-tailed shearwaters in the continental shelf area of the northeastern Bering Sea, from Cape Navalin (Russia) to the Pribilof Islands (USA). There they found the hyperiid amphipod *Themisto libellula* to be the dominant prey by frequency of occurrence (69.6%) and by weight, accounting for 69.1% of the total stomach contents by weight. We are unaware of any short-tailed shearwater diet studies specific to the Chukchi Sea, and in their absence we use a generalized diet adapted from the diet described by Ogi et al. (1980) for short-tailed shearwaters occupying the northeastern Bering Sea. There the fish prey were identified as walleye pollock and capelin. To adapt this diet to the Chukchi Sea, we replace the portion allocated to walleye pollock with Arctic cod. Walleye pollock is the dominant schooling, bentho-pelagic gadid in the eastern Bering Sea, while Arctic cod fulfills a similar role in the eastern Chukchi Sea. The diet we used for short-tailed shearwaters consists of 88% other zooplankton (primarily hyperiid amphipods and euphausiids), 6% pelagic forage fish, and 6% Arctic cod.

The functional group diet composition is an average diet weighted by the biomass of the constituent species. The primary prey of the Procellarid group is other zooplankton (86.5%), followed by Arctic cod (7%), pelagic forage fish (5.9%), copepods (0.4%), and benthic amphipods (0.2%).

Cormorants

Cormorants are represented by a single species, the pelagic cormorant (*Phalacrocorax pelagicus*), in colony counts from the eastern Chukchi Sea (Swartz 1966, Seabird Information Network 2011).

Updated parameters

Biomass (B): The biomass of pelagic cormorants is estimated from colony count data (Seabird Information Network 2011) and a mean individual body mass of 1.868 kg (Hunt et al. 2000). The functional group biomass is 1.469 $*10^{-6}$ t km^{-2}.

Production (P/B): In lieu of a species-specific annual survival rate, we used an Order level (Charadriiformes) estimated adult survival rate of 0.85 to calculate a group P/B of 0.1625.

Consumption (Q/B): The cormorant Q/B of 142.618 was calculated assuming a mean individual body mass of 1.868 kg and a daily energy requirement of 2737.102 kj (Hunt et al. 2000).

Food habits (DC): Pelagic cormorants forage by diving for prey, using their feet for propulsion under water (Hobson 1997). The diet of pelagic cormorants collected from the Pribilof Islands was dominated by fishes (74%), primarily sculpins (*Myoxocephalus* spp. and *Megalocottus laticeps*) (Preble and McAtee 1923). The remainder of the diet consisted of crustaceans, primarily shrimp (*Spirontocaris* spp.) and anomuran crabs. Ainley and Sanger (1979) summarized diet records of pelagic cormorants from multiple diet studies conducted in the northeast Pacific and Bering Sea, and found sculpins (Cottidae) and decapods to be major prey items throughout their range. Other prey items from Alaska included herring (*Clupea* sp.), cods (Gadidae), greenlings (Hexagrammidae), poachers (Agonidae), gunnels (Pholidae), Pacific sand lance (*Ammodytes hexapterus*), and flatfish (Pleuronectidae). In the eastern Chukchi Sea, Swartz (1966), examined two pelagic cormorant stomachs and found fish (Arctic cod [*Boreogadus saida*], Pacific sand lance, and Stichaeidae) and shrimp (Pandalidae and Crangonidae) to be the primary prey. Lacking a more detailed region-specific and species-specific diet description, we use the diet provided by

Swartz (1966) as the basis for our pelagic cormorant diet. We divide the diet evenly (25% each) between Arctic cod, pelagic forage fish (Pacific sand lance), miscellaneous shallow fish (Stichaeidae), and shrimp.

Scolopacids

Scolopacidae is a family of shorebirds that includes sandpipers, snipes, dowitchers, and phalaropes, among others. We focus our interest on two species of phalarope, the red phalarope (*Phalaropus fulicaria*) and red-necked phalarope (*P. lobatus*). These two species spend only the short breeding season on land, then spend the rest of the year (9 months or more) living at sea, and eating marine prey (Höhn 1969, Rubega et al. 2000, Schreiber and Burger 2001, Tracy et al. 2002). The red and red-necked phalaropes are the only shorebirds to spend such a significant portion of their lives at sea (Schreiber and Burger 2001). The two species are difficult to discern during at-sea observations and are frequently referred to collectively in the literature as phalaropes or *Phalaropus* sp. (e.g., Gall et al. 2013). Phalaropes are among the most abundant seabirds observed in the pelagic environment of the Chukchi Sea during the ice-free season (Divoky 1987, Piatt and Springer 2003, Gall et al. 2013).

Updated parameters

Biomass (B): The biomass estimate for Scolopacids was calculated from the populations estimates in Divoky (1987). At peak abundance during the ice-free season, Divoky (1987) estimated there to be about 1,000,000 phaloropes present. Because the abundance estimate is not species-specific we used a mean individual body mass of 44.75 g, calculated from species-specific body masses provided in Hunt et al. (2000). The estimated biomass of the Scolopacid group is $7.77*10^{-5}$ t km^{-2} (Table 5).

Production (P/B): Species-specific survival rates were not available for this group and instead we use an Order level (Charadriiformes) estimated adult survival rate of 0.85 (Schreiber and Burger 2001). The functional group P/B is 0.1625.

Consumption (Q/B): Q/B was estimated for the red-necked and the Red phalarope assuming mean individual body masses of 33.8 g and 55.7 g, respectively. The functional group Q/B of 374.313 is an average of the two species-specific Q/Bs.

Food habits (DC): In the open ocean, phalaropes feed in surface waters where oceanographic conditions concentrate their prey within their reach at the ocean surface. They feed by pecking their bill into the water and use the surface tension of water to deliver the prey into their mouth (Rubega and Obst 1993). They feed predominantly on copepods, euphausiids, fish eggs, other meroplankton, and other crustacean zooplankton (Briggs et al. 1984, Divoky 1984, Mercier and Gaskin 1985, Brown and Gaskin 1988). They have also been observed to feed on benthic amphipods in the mud plumes brought to the surface by benthic foraging gray whales in the northern Bering Sea (Obst and Hunt 1990, Grebmeier and Harrison 1992). The density of phalaropes has been positively correlated with whale density in the northern Bering Sea, indicating association with whales may provide an important food source for phalaropes in this region (Obst and Hunt 1990). Divoky (1984) presented diet data on red phalaropes collected in the pelagic and nearshore Beaufort Sea, Alaska, and found the stomachs to most frequently contain amphipods, copepods, and other zooplankton. Lacking diet information specific to the Chukchi Sea or a more general region-wide diet description, we attribute 10% of the diet to benthic amphipods and evenly divide the rest of the diet among copepods (45%) and other zooplankton (45%).

Larids

The Larids functional group consists of species from the family Laridae. In the eastern Chukchi Sea this group is dominated numerically and by weight by the black-legged kittiwake (*Rissa tridactyla*), followed by the glaucous gull (*Larus hyperboreus*). Also present in colony counts, but in much lower abundance, are Arctic terns (*Sterna paradisaea*), Aleutian terns (*S. aleutica*), and mew gulls (*L. canus*). Other species known to occur in the eastern Chukchi Sea include ivory gull (*Pagophila eburnean*), Sabine's gull (*Xema sabini*), Ross's gull (*Rhodostethia rosea*), and herring gull (*L. argentatus*) (Swartz 1966, Divoky 1987, Gall et al. 2013).

Updated parameters

Biomass (B): The estimated biomass of the Larid group is calculated with colony counts (Seabird Information Network 2011) and species-specific estimates of mean individual body mass (Hunt et al. 2000). The estimated functional group biomass is $9.313 * 10^{-5}$ t km^{-2} (Table 5).

Production (P/B): Species-specific annual survival rates were available for black-legged kittiwake (0.88-0.93) and Arctic terns (0.90). An order level (Charadriiformes) adult survival rate of 0.85 was assumed for mew gull, glaucous gull, and Aleutian tern. The functional group P/B of 0.1057 is a mean P/B weighted by the estimated biomass of the constituent species.

Consumption (Q/B): The Q/B of Larids (Table 7) is calculated assuming species-specific mean individual body masses and daily energy needs taken from Hunt et al. (2000). The functional group Q/B of 205.67 is an average Q/B weighted by the estimated biomass of the constituent species.

Food habits (DC): Glaucous gulls are generalist feeders whose diet includes fish, zooplankton, other crustaceans, birds, mammals, and insects (Weiser and Gilchrist 2012). In the Beaufort Sea glaucous gulls consumed Arctic cod, other seabirds, and amphipods (Divoky 1984). The seabird prey was identified as phalaropes and accounted for 75% of the total prey weight (Divoky 1984). In the eastern Chukchi Sea, the diet of glaucous gulls collected near seabird colonies included Arctic cod, sand lance, *Myoxocephalus quadricornis*, murres, kittiwakes, anemones, crabs, unidentified crustaceans, insects, and mammals (Swartz 1966). The carcasses of birds that have died from rockfalls and the eggs of other bird species may form an important part of the glaucous gull diet in the eastern Chukchi Sea (Swartz 1966). The remains of murre chicks occurred in 50% of the glaucous gull stomachs examined (excluding nestlings) (Swartz 1966). The diet of glaucous gulls nesting on the coast of the eastern Bering Sea most frequently included fish (primarily saffron cod [*Eleginus gracilis*]), birds (mostly eggs), and marine invertebrates (Strang 1982). Bird remains and bird eggs were also frequently observed among the prey remains found in regurgitated pellets collected from glaucous gull colonies in the Beaufort Sea (Barry and Barry 1990). The remains of juvenile birds were found among the stomach contents of five glaucous gulls collected during summer from the Frans Josef Land Archipelago in the Russian Arctic (Weslawski et al. 1994). The juvenile bird prey accounted for more than 91% of the total prey weight and included thick-billed murres, kittiwakes, and dovekies (Weslawski et al. 1994). The large proportion of bird prey in the diet of glaucous gulls may overestimate the proportion of bird prey in the diet of glaucous gulls found in the pelagic environment, as most of the existing diet studies were either shore-based or conducted within the vicinity of seabird colonies where bird prey would be in greater abundance (Weiser and Gilchrist 2012). There is very limited information available describing the diet of glaucous gulls while at sea (Weiser and Gilchrist 2012) but fish appear to be a principal part of their diet throughout their range. The diet of glaucous gulls is regularly reported to include bird remains, including eggs, chicks, juveniles, and adults (e.g., Swartz 1966); though predation on uninjured adults is an uncommon occurrence and these are most likely scavenged (Mallory et al. 2009, Weiser and Gilchrist 2012). More frequently glaucous gulls are consuming eggs, chicks, injured birds, or birds already dead from rockfalls or other circumstances. Eggs are not modeled as separate functional groups and represent losses from seabirds to respiration, or in other words a loss to detritus. Dead birds or injured and soon-to-be dead birds also represent a flow to detritus. Glaucous gulls preying on these sources are effectively feeding off of the detrital pool as opposed to depredating other seabird functional groups directly. In the eastern Chukchi Sea, murres were the principle seabird prey of glaucous gulls at seabird colonies (Swartz 1966). Lacking detailed information on the glaucous gull diet we attribute 5% to direct predation on murres (Alcids piscivorous) and 20% to detritus according to the detrital fate of seabirds (6% pelagic detritus, 14% benthic detritus). In lieu of a quantitative description of the pelagic diet of glaucous gulls, we divide the remaining 75% of the diet evenly (25% each) amongst Arctic cod, saffron cod, and pelagic forage fish (sand lance).

The diet of mew gulls varies with location and season (Moskoff and Bevier 2002) and is not described in the eastern Chukchi Sea. In other parts of their range they consume a variety of prey including fish, crabs, mollusks, polychaetes, and zooplankton, also terrestrial foods including birds (swallows and sparrows), mammals, insects, garbage, and sewage (Moskoff and Bevier 2002, Kubetzki and Garthe 2003). We use a general diet for mew gulls adapted from the diet reported by Sanger (1986) for mew gulls collected in the Gulf of Alaska and adjacent regions. Amphipods (58.1%), shrimp (23%), pelagic forage fish (16.5%), bivalves (1%), Arctic cod (1%), polychaetes (0.3%), and snails (0.1%) comprise the final diet.

Arctic terns are opportunistic foragers that feed primarily on fish, particularly pelagic forage fish and gadids, but also prey on invertebrates including amphipods, decapods, euphausiids, and polychaetes (Hatch 2002). The diet of Arctic terns collected offshore in the Beaufort Sea were dominated by weight by Arctic cod (64%), followed by euphausiids (35%) and amphipods (1%) (Divoky 1984). Near shore they fed upon (by % weight) euphausiids (23%), amphipods (31%), Arctic cod (20%), mysids (13%), and Pacific sand lance (12%). The diet of Arctic terns collected from Frans Josef Land Archipelago were dominated by amphipods (74.9% by weight), followed by unidentified fish remains (20.9%), and polychaetes (4.2%). Lacking a diet specific to the eastern Chukchi Sea, we use the diet of Arctic terns collected from offshore waters in the Beaufort Sea (Divoky 1984) as a proxy for their diet in the eastern Chukchi Sea. The final diet is 64% Arctic cod, 35% other zooplankton, and 1% amphipods.

The primary prey items of Aleutian terns are fish, including Pacific sand lance, capelin, and gadids. They also prey on invertebrates including decapods, euphausiids, isopods, polychaetes, and insects (North 1997). During spring and summer in the southeastern Bering Sea, Aleutian terns preyed primarily upon fish (75-98% by weight) and euphausiids (25%) (Troy and Johnson 1989). Near Kodiak Island in the Gulf of Alaska, the diet of adult Aleutian terns contained (% by weight) euphausiids (54.7%), isopods (11.4%), arthropods (1.8%), insects (1.4%), Pacific sand lance (12.2%), capelin (7.3%), Gadidae (5.5%), and unidentified fish (5.6%) (Sanger 1986). We are unaware of any Aleutian tern diet records from the eastern Chukchi Sea and in their place we use a general diet adapted from the diet reported by Sanger (1986). The diet we used consists of other zooplankton (58%), pelagic forage fish (21%), miscellaneous crustaceans (14%), Arctic cod (6%), and polychaetes (0.1%).

The Larid group diet is an average diet weighted by the estimated biomass of the constituent species within the model area. The primary prey items for Larids are Arctic cod (50.1%) and pelagic forage fish (33.3%). Prey groups of lesser importance include benthic amphipods (3.5%), other zooplankton (2.6%), polychaetes (2.4%), saffron cod (2.3%), detritus (1.9%), and shrimps (1.1%). Prey groups that individually represent less than 1% of the final Larid diet include snails, other crabs, Alcids piscivorous, miscellaneous shallow fish, snailfish, variegated snailfish, large-mouth sculpins, Other sculpins, and miscellaneous crustaceans.

Alcids piscivorous

Six species from the family Alcidae, whose diets are dominated (> 50%) by fish prey, comprise the Alcids-piscivorous group. The group contains two species of murre (*Uria* spp.), two species of puffin (*Fratercula* spp.), and two species of guillemot (*Cepphus* spp.).

Updated parameters

Biomass (B): Abundance estimates for all six species are derived from colony counts contained in the North Pacific Seabird Colony Database (Seabird Information Network 2011). The two species of murre, the common murre (*Uria aalge*) and thick-billed murre (*U. lomvia*), are the numerically dominant members of this group and also make the greatest contribution to group biomass. Additionally, murres are augmented by colony counts of unidentified murres. The total count for all colonies for each species is multiplied by a species-specific mean body mass (Hunt et al. 2000) to arrive at a biomass estimate. This estimate is then divided by the model area to calculate a biomass density estimate (t km^{-2}). This is reduced further by multiplying by one-third to account for the seasonal occupation (~4 months) of the model area. Alcids piscivorous have a B of 0.0012 t km^{-2}.

Production (P/B): The Alcids piscivorous P/B is calculated from species-specific annual survival rates (Schreiber and Burger 2001). When survival rate is given as a range the midpoint is used. Species-specific estimates were not available for the tufted puffin or horned puffin. So, in their place we use an annual survival rate for the Atlantic puffin (*Fratercula arctica*). For unidentified murres we used the average of the thick-billed murre and common murre survival rates, weighted by their estimated biomass. The functional group P/B of 0.1041 is a weighted average P/B (by biomass).

Consumption (Q/B): The Alcids piscivorous Q/B of 178.383 is an average of the constituent species Q/Bs, weighted by biomass.

Food habits (DC): Common and thick-billed murres forage in the pelagic environment by diving for prey. Swartz (1966) examined stomachs from both species at nesting colonies in the Cape Thompson region and found fish to be the dominant component of the diet for both species. Arctic cod (*Boreogadus saida*) was the most frequently occurring prey, followed by Pacific sand lance (*Ammodytes hexapterus*). Other frequently encountered prey included sculpins, Stichaeids, hermit crabs (thick-billed murres only), snails (thick-billed murres only), polychaetes, and shrimps. Springer et al. (1984) examined the diet of common and thick-billed murres at two breeding colonies in the eastern Chukchi Sea at Cape Lisburne and Cape Thompson, between 1976 and 1980. For both species at both locations, the dominant prey items by weight were cods (Arctic cod and saffron cod [*Eleginus gracilis*]) followed by pelagic forage fish (sand lance and capelin [*Mallotus villosus*]). In all years of the study, Arctic cod represented the majority of the gadids taken by murres in mid- to early summer, while saffron cod were the dominant gadid prey in late summer (Springer et al. 1984). Other fish prey of lesser importance included sculpins and flatfish. Invertebrate prey were also consumed by both species but figured more prominently in the diet of thick-billed murres. Invertebrate prey items included shrimps, amphipods, euphausiids, polychaetes, hermit crabs, and snails. The diet of common and thick-billed murres nesting at Cape Thompson were examined again in the summer of 1988 by Fadely et al. (1989). Fish were again the dominant prey items, with Arctic cod accounting for 94% of the prey by weight for both species. Of lesser importance were saffron cod, sand lance, and sculpins. Invertebrate prey were only found in the stomachs of thick-billed murres and collectively accounted for less than 1% of stomach contents by weight. The invertebrate prey included shrimps, amphipods, and gastropods. Hunt et al. (1981) summarized the prey of common and thick-billed murres breeding on the Pribilof Islands in the eastern Bering Sea and also found fish to be the most important part of the murre diet. Both species fed heavily on the dominant gadid of the region, walleye pollock (*Gadus chalcogrammus*).

The murre diet used here is derived from the values reported in Springer et al. (1984). The percent composition of the diet by weight reported for each study location in tables 2 &3 of Springer et al.

(1984) were averaged for each species, weighted by the sample size at each location (total stomachs examined). The taxonomic categories of prey items reported by Springer et al. (1984) did not always taxonomically match the functional groups used in our model. Some prey groups needed to be divided to match more taxonomically narrow groups within our model, while others needed to be combined to fit more general groupings (Table 3). The prey categories of cods, sculpins, and other invertebrates had to be divided amongst existing functional groups in our Ecopath model. The portion of the diet Springer et al. (1984) allocated to "cods" was divided up evenly amongst Arctic cod and saffron cod; the only two gadids reported to occur in the murre diet in their study region (Springer et al. 1984, Fadely et al. 1989). Similarly, the "sculpin" portion of the diet was also divided evenly among our two sculpin functional groups, large-mouth sculpins and Other sculpins. The "other invertebrate" category included snails and hermit crabs and was divided evenly between the snail and other crabs functional groups. Prey categories reported by Springer et al. (1984) that needed to be combined included two forage fish species, Pacific sand lance and capelin. The percent compositions for these two species were combined to fit within the pelagic forage fish functional group. The euphausiids and mysids portion of the diets were also combined to fit within the "other zooplankton" functional group. The dominant prey items in the final diets for both species are Arctic cod, saffron cod, pelagic forage fish, large-mouth sculpins, and Other sculpins.

Two species of puffin are found in the eastern Chukchi Sea: the horned puffin (*Fratercula corniculata*) and tufted puffin (*F. cirrhata*). Horned puffins are the more prevalent of the two species, accounting for more than 97% of the total puffins in colony counts of the eastern Chukchi Sea region (Seabird Information Network 2011). Both species of puffin can be found in the pelagic environment, where they forage for their prey by diving. Hunt et al. (2000) attributed ~80% of the diet of horned and tufted puffins, found in the vicinity of the Pribilof Islands, to fish prey. The major prey item for the horned puffin was whitespotted greenling (*Hexagrammos stelleri*), and for the tufted puffin the major prey was walleye pollock. Both species of puffin also preyed on pelagic forage fish (Pacific sand lance and capelin), and the horned puffin additionally preyed upon the Pacific sandfish (*Trichodon trichodon*). Both species of puffins also consumed invertebrate prey including pelagic amphipods (*Parathemisto libellula*) , polychaete worms (Nereidae), and cephalopods (Hunt et al. 1981). The stomachs of horned puffins collected at Cape Thompson in the eastern Chukchi Sea were found to contain Arctic cod, capelin, Pacific sand lance, sculpins (*Triglops* sp.), polychaetes, sponge (Porifera) and unidentified crustaceans (Swartz 1966). Because horned puffins are the numerically dominant species of puffin in the eastern Chukchi Sea, their diet as described by Hunt et al. (1981) and Hunt et al. (2000) is used here to describe the feeding habits of both species of puffin. The prey categories of Hunt et al. (2000) are broader than the functional groups used in this model and not all prey taxa are listed in Hunt et al. (1981). To accommodate this difference, the 80% of the diet attributed to fish by Hunt et al. (2000) is divided evenly (40% each) amongst the primary fish prey categories of pelagic forage fish and Arctic cod. Pelagic amphipods (other zooplankton) account for 11% of the diet and polychaetes 4%. The remaining 5% of prey are listed as “unknown” in Hunt et al. (2000). Because we are unable to attribute this small amount to any one prey group, we exclude it and renormalize the diet to one. The diet we used for puffins consists of pelagic forage fish (42.1%), Arctic cod (42.1%), polychaetes (11.6%), and other zooplankton (4.2%).

Black guillemots forage for their prey by diving into the water and using their wings to swim under water (Butler and Buckley 2002). They prey primarily upon fish and may also consume benthic and sympagic invertebrates (Butler and Buckley 2002). Black guillemot stomachs collected from ice-covered waters near Svalbard contained fish, gammarid amphipods, and mysids (Lønne and Gabrielsen 1992). Of the fish prey, 72% of the otoliths found in the stomachs were identified as Arctic cod (Lønne and Gabrielsen 1992). Similarly, black guillemot stomachs collected from the Franz Josef Land Archipelago were dominated by Arctic cod, accounting for 88.1% of total stomach contents by weight (Weslawski et al. 1994). Other prey of lesser importance (by % weight) included shrimp (4.7%), *Myoxocephalus scorpius* (2.9%), unidentified fish (2.9%), and amphipods (1.3%). In pelagic ice-covered areas near Svalbard, the diet of black guillemots was dominated by Arctic cod which occurred in 71.4% of stomachs examined (Mehlum and Gabrielsen 1993). In coastal waters their diet was more diverse and included polychaetes, decapods, amphipods, gastropods, copepods, and euphausiids. In the Canadian High Arctic the diet of black guillemots collected near breeding colonies on Devon Island included crustaceans (amphipods and mysids), fish (Arctic cod, *Liparis tunicatus*, and sculpins [Cottidae]), polychaetes, gastropods, and cephalopods (Byers et al. 2010). A single black guillemot stomach collected in the eastern Chukchi Sea contained Arctic cod and polychaetes (Swartz 1966). The diet of black guillemots consistently features fish as prominent part of the diet, especially Arctic cod. Lacking more region-specific information we use the diet presented in Weslawski et al. (1994) for black guillemots. The diet we used includes Arctic cod (90%), large-mouth sculpins (3%), shrimp (4.7%), and amphipods (2.3%).

Pigeon guillemots forage for prey by diving and using their wings to swim under water (Ewins 1993). They feed primarily on benthic and demersal fish and invertebrate prey but may also catch schooling fish in the water column or near the surface (Ewins 1993, Litzow et al. 2000). Reported fish prey of the pigeon guillemot in Alaska include pelagic forage fish (Pacific sand lance, capelin), salmonids, cods (Gadidae), sculpins (Cottidae, *Myoxocephalus* sp.), Pacific sandfish (*Trichodon trichodon*), pricklebacks (Stichaeidae), gunnels (Pholidae), ronquils (Bathymasteridae), and flatfish (Pleuronectidae) (Sanger 1986, Litzow et al. 2000). Identified invertebrate prey of pigeon guillemots in Alaska include shrimps (Hippolytidae, Pandalidae, Crangonidae), crabs (Anomura [Paguridae, Hapalogastridae], Brachyurans [Oregoniidae, Cheiragonidae, Cancridae]), gammarid amphipods, mysids, polychaetes, bivalves, and snails (Sanger 1986, Litzow et al. 2000). Lacking a diet description specific to the Chukchi Sea, we use a general diet adapted from the diet reported (by % volume) by Sanger (1986).

The final functional group diet for Alcids piscivorous is an average diet weighted by the estimated biomass of the constituent groups. The group diet composition is dominated by fish groups including pelagic forage fish (27.3%), Arctic cod (26%), saffron cod (23.7%), large-mouth sculpins (7.1%), Other sculpins (7.1%), small-mouth flatfish (1.9%), miscellaneous shallow fish (0.3%), snailfish (0.3%), and the variegated snailfish (0.3%). The most prominent invertebrate prey groups are benthic amphipods (2.3%), other zooplankton (1.1%), and shrimp (1%). The remainder of the diet consists of polychaetes, other crabs, snails, and bivalves.

Alcids planktivorous

The Alcids planktivorous functional group consists of four species from the family Alcidae, whose diets are dominated by zooplankton (> 50%). The four species representing this group are the parakeet auklet (*Aethia psittacula*), least auklet (*A. pusilla*), crested auklet (*A. cristatella*), and the dovekie (*Alle alle*).

Updated parameters

Biomass (B): Abundance estimates for all four species are derived from colony counts contained in the North Pacific Seabird Colony Database (Seabird Information Network 2011). Numerically, the group is dominated by crested auklets (219,000) and least auklets (207,000). Species of lower abundance in colony counts are the parakeet auklet (20,000) and dovekie (50). The abundance estimates were used in combination with estimates of average individual body mass from Hunt et al. (2000) to arrive at a group biomass of 0.00014 t km-2 (Table 5).

Production (P/B): The Alcids planktivorous P/B of 0.1404 was calculated from both species-specific estimates of annual survival and from an Order-level estimate of adult survival (Schreiber and Burger 2001). An annual survival rate of 0.89 was used for the crested auklet and 0.808 for the least auklet. An order level (Charadriiformes) adult survival rate of 0.85 was used for parakeet auklet and dovekie. The functional group P/B is an average P/B, weighted by biomass.

Consumption (Q/B): Alcids planktivorous have a weighted (by biomass) average Q/B of 247.507.

Food habits (DC): Least auklets feed primarily by diving and using their wings for propulsion under water (Ainley and Sanger 1979, Bond et al. 2013). During summer they prey almost exclusively on crustacean zooplankton, with limited reports of larval fish or fish otoliths among prey items (Bond et al. 2013). Calanoid copepods are the principal prey of least auklets throughout their range in the north Pacific Ocean and Bering Sea during summer (Bedard 1969, Hunt et al. 1981, Springer and Roseneau 1985, Gall et al. 2006, Sheffield Guy et al. 2009, Bond et al. 2013). Other prey items include euphausiids, gammarid amphipods, hyperiid amphipods, and decapod larvae (Bedard 1969, Hunt et al. 1981, Springer and Roseneau 1985, Harrison 1990, Gall et al. 2006, Sheffield Guy et al. 2009). In lieu of diet data specific to the eastern Chukchi Sea, we use a general diet adapted from data (% biomass) presented in Gall et al. (2006) and Sheffield Guy et al. (2009) for least auklets sampled in the northern Bering Sea. The least auklet diet used here consists of 75% copepods and 25% other zooplankton (including decapod larvae, hyperiids, euphausiids, pteropods, and larval fish).

Crested auklets feed by diving and pursuing their prey under water using their wings for propulsion (Ainley and Sanger 1979, Jones 1993). During summer the diet of crested auklets primarily consists of crustacean zooplankton, in particular euphausiids (Bedard 1969, Hunt et al. 1981, Jones 1993, Gall et al. 2006, Sheffield Guy et al. 2009). Other prey items taken during summer in the Bering Sea and Aleutian Islands include copepods, amphipods, shrimp, fish, jellyfish, pteropods, and cephalopods (Harrison 1990, Hunt et al. 1998, Gall et al. 2006, Sheffield Guy et al. 2009). Lacking diet data specific to the eastern Chukchi Sea, we use a general diet adapted from data presented (by % biomass) in Gall et al. (2006) and Sheffield Guy et al. (2009) for crested auklets sampled in the northern Bering Sea. The diet we used here is 25% copepods and 75% other zooplankton (including decapod larvae, hyperiids, euphausiids, pteropods, and larval fish).

Parakeet auklets feed by diving and using their wings for propulsion under water (Ainley and Sanger 1979). The summer diet of the parakeet auklet is more general than the diet of least and crested auklets and includes pteropods, euphausiids, larval fish, gelatinous zooplankton (Ctenophora and Scyphomedusae), polychaetes, amphipods, and copepods (Bedard 1969, Hunt et al. 1981, Harrison 1990, Hunt et al. 1998). In the Chirikov Basin, north of St. Lawrence Island and south of Bering Strait, gelatinous zooplankton were an important part of the diet and may be a preferred prey item (Harrison 1990). Similarly, gelatinous zooplankton was the predominant part of the diet of parakeet auklets collected during summer in the western Aleutian Islands (Hunt et al. 1998). In the absence of diet data specific to the eastern Chukchi Sea, we adapt a general diet from the values reported by % weight in Hunt et al. (1981) and by frequency of occurrence in Harrison (1990) and Hunt et al. (1998). Other zooplankton (60%), jellyfish (30%), and copepods (10%) comprise the final diet.

In coastal waters and in the pelagic marginal ice zone (MIZ) near Svalbard, the diet of dovekies was dominated by copepods in both frequency of occurrence and total numbers (Mehlum and Gabrielsen 1993). Copepods accounted for 85% of the diet by percent weight during summer in the coastal zone. The second and third most prominent prey items in the coastal area by percent weight were decapod larvae and hyperiid amphipods. Other prey items taken near Svalbard include gastropods, gammarid amphipods, chaetognaths, and larval fish. Similarly, the diet of dovekies at Bear Island (Bjørnøya, Norway) in the Barents Sea was dominated by copepods, accounting for more than 69% of food biomass, followed by decapod larvae (22%), and amphipods (5%) (Weslawski et al. 1999). In the Frans Josef Land Archipelago of the Russian Arctic, dovekie diet was also dominated by copepods, accounting for 72% of the diet by weight and 84% by number (Weslawski et al. 1994). Other important prey groups (by % weight) are euphausiids (12.6%), gammarid amphipods (13%), mysids (0.7%), and larval fish (0.3%). Lacking diet data specific to the eastern Chukchi Sea, we use a general diet for dovekies adapted from the data presented in Weslawski et al. (1994) and Mehlum and Gabrielsen (1993), with 75% of the diet consisting of copepods and 25% other zooplankton (includes mysids, hyperiids, decapod larvae, gastropods [pteropods], chaetognaths, and larval fish).

The functional group diet is an average diet weighted by the biomass estimated for each of the constituent species. Other zooplankton (63.2%), copepods (34.9%), and jellyfish (1.9%) comprise the final diet for the Alcids planktivorous group.

Fish

All fish functional groups

Biomass (B)

Survey-derived estimates of biomass for most of the fish groups were insufficient to meet predator demands and balance the model (i.e., EE > 1). As a result we top-down balanced biomass for 11 of the 16 fish groups, assuming EE = 0.8 (Table 2). Alaska skate, walleye pollock, Pacific cod, salmon outgoing, and salmon returning were not top-down balanced.

Production (P/B) and consumption (Q/B)

Estimates of P/B and Q/B were updated for all four gadid species (Arctic cod, saffron cod, Pacific cod, and walleye pollock), and for both large-mouth and small-mouth flatfish. P/B and Q/B are unchanged from the preliminary model for all other fish functional groups.

Food habits (DC)

The diet compositions of most fish functional groups were updated with food habits data gathered during Arctic Eis trawl surveys (Table 4).

Large-mouth flatfish

Three species from the family Pleuronectidae, Bering flounder (*Hippoglossoides robustus*), Greenland turbot (*Rheinhardtius hippoglossoides*), and Pacific halibut (*Hippoglossus stenolepis*) comprise the large-mouth flatfish group. All three of these species have large mouths relative to other Arctic flatfish (e.g., yellowfin sole, longhead dab, others) and fish are a featured part of their diet.

Updated parameters

Biomass (B): Adding Bering flounder to the large-mouth flatfish group substantially increased the estimated biomass for this group as neither Greenland turbot nor Pacific halibut are abundant in the eastern Chukchi Sea. Small numbers of Greenland turbot and Pacific halibut were previously observed during trawl surveys of the eastern Chukchi Sea in 1976 (Wolotira et al. 1977) and 1990 (Barber et al. 1997). During the 2012 Arctic Eis bottom trawl survey, only a single Greenland turbot was caught (weight 0.01 kg, length 10 cm) and no Pacific halibut were encountered (Goddard et al. 2014). Bering flounder were substantially more abundant with more than 2.5 individuals per hectare (Goddard et al. 2014). Bering flounder compose more than 99.9% of the initial biomass input of 0.0095 t km^{-2} for this group. The addition of Bering flounder to this group also increased the pressure from predators as Bering flounder are present in the diets of seals, seabirds, and other fishes. As a result, the trawl survey-derived biomass estimate was insufficient to meet predator demands and biomass was therefore top-down balanced (EE = 0.8), which produced a biomass estimate of 0.1114 t km^{-2}.

Production (P/B): Region-specific information required to calculate P/B and Q/B for this functional group are available only for Bering Flounder. P/B is calculated with a regression of estimator of mortality (Hewitt and Hoenig 2005) under the assumption that under steady-state conditions P/B is equal to mortality, Z (Allen 1971). This method requires an estimate of maximum age (11) which we acquired from Smith et al. (1997). P/B is estimated to equal 0.401.

Consumption (Q/B): Q/B was calculated following the methods of Aydin (2004) which requires an estimate of mortality (Z) and the parameter *k* from the von Bertalanffy growth function (vBGF). Mortality was taken from the aforementioned P/B calculation (0.401) and k was taken from Smith et al. (1997) resulting in Q/B = 1.78.

Food habits (DC): Region-specific diet information is extremely limited for Greenland turbot and is unavailable for Pacific halibut. A single Greenland turbot stomach was collected during the 2012 Arctic Eis bottom trawl survey. The turbot was 10 cm long and the stomach contained two cumaceans and one euphausiid. Sampling of Bering flounder stomachs was more fruitful, with 94 (non-empty) stomachs collected during the 2012 survey. Due to the lack of adequate sample size for Greenland turbot and Pacific halibut, the diet composition used for large-mouth flatfish is that of Bering flounder. Coyle et al. (1997) found the diet of Bering flounder captured near Pt. Hope to be dominated by fish. The most important identified fish prey was *Lumpenus* sp. (Stichaeidae, miscellaneous shallow fish), other prey fish families included eelpouts, poachers (misc. shallow fish), sculpins, and cods. Similarly from our stomach collections in the eastern Chukchi Sea, the Bering flounder diet composition consists of 33% miscellaneous shallow fish (Stichaeids), 24% Arctic cod, 20% shrimp, 14.5% other zooplankton, 5% polychaetes, 2.5% benthic amphipods, <1% bivalves, and <1% copepods.

The prey items contributing to the Arctic cod portion of the diet were identified as Gadidae when the stomach contents were analyzed in the lab. In the adjacent eastern Bering Sea, about 52% of the Bering flounder diet (n = 830 non-empty stomachs) is walleye pollock, the dominant semi-pelagic gadid of that region. Walleye pollock are present in extremely low numbers in the Chukchi Sea. In the absence of information to guide how to divide the Gadidae portion of the Bering flounder diet up amongst our four gadid groups in the eastern Chukchi Sea, we have assigned all the prey identified as Gadidae to the dominant gadid (most abundant and highest biomass) of the region, Arctic cod.

Small-mouth flatfish

The small-mouth flatfish group is represented by six species from the family Pleuronectidae, yellowfin sole (*Limanda aspera*), longhead dab (*L. proboscidea*), Sakhalin sole (*L. sakhalinensis*), Arctic flounder (*Liopsetta glacialis*), starry flounder (*Platichthys stellatus*), and Alaska plaice (*Pleuronectes quadrituberculatus*). All of these species are found in the benthic environment and their primary prey items are benthic invertebrates.

Updated parameters

Biomass (B): Removing Bering flounder from this group reduced their trawl survey based biomass estimate to 0.0694 t km^{-2}, from 0.0799 t km^{-2}. The predation pressure from higher trophic levels was also reduced; however, a top-down balance of biomass was still required to meet predator demands. This resulted in a biomass estimate of 0.0902 t km^{-2} (EE = 0.8).

Production (P/B): Under equilibrium conditions, P/B is assumed to be equal to mortality (Z) (Allen 1971). Following this relationship, P/B was calculated with the regression estimator of mortality from Hewitt and Hoenig (2005). This method requires only a single input, an estimate of maximum age. Estimates of maximum age for yellowfin sole, starry flounder, and Alaska plaice were taken from Wolotira et al. (1977). Estimates of P/B for longhead dab and Sakhalin sole were taken from the Ecopath model of the eastern Bering Sea (Aydin et al. 2007). An estimate of P/B, or the data required to calculate it, was not available for Arctic flounder, so the other species in this group are taken as representative of this species. The functional group P/B of 0.308 is an average P/B, weighted by the estimated biomass of the constituent species from the 2012 survey.

Consumption (Q/B): Q/B was calculated following the methods of Aydin (2004) which requires an estimate of mortality (Z) and the growth parameter *k* from the von Bertalanffy growth function (vBGF). Estimates of mortality were taken from the aforementioned P/B calculations. The vBGF parameter *k* was taken from Wolotira et al. (1977) for yellowfin sole, starry flounder, and Alaska plaice. Estimates of longhead dab and Sakhalin sole Q/B are taken from the eastern Bering Sea Ecopath model (Aydin et al. 2007). The required information was not available to calculate Q/B for Arctic flounder, so the other members of this group are taken as representative for this species. The final group Q/B of 1.535 is an average Q/B, weighted by biomass estimates derived from the 2012 survey.

Food habits (DC): The diet composition is derived from stomach collections made during the 2012 trawl surveys (Table 4). The final diet is an average diet weighted by biomass. The diet composition for small-mouth flatfish is 37% bivalves, 35% polychaetes, 12% benthic amphipods, 5% urchins, dollars, cucumbers, 4% miscellaneous crustaceans, 3% brittle stars, 3% snow crab, and 1% worms, etc. The diet also includes traces (<1%) of snails, other crabs, and copepods.

Large-mouth sculpin

This group of sculpins is represented by six species from two genera of the family Cottidae; *Hemilepidotus papilio* (butterfly sculpin), *Myoxocephalus scorpius* (shorthorn [warty] sculpin), *M. jaok* (plain sculpin), *M. polyacanthocephalus* (great sculpin), *M. quadricornis* (fourhorn sculpin), and *M. scorpioides* (Arctic sculpin). Although marine fishes of the Chukchi Sea are generally small in size (Norcross et al. 2010, Goddard et al. 2013, Goddard et al. 2014), these two genera are grouped together in part because they commonly grow to large sizes in other parts of their range in Alaska (e.g., the eastern Bering Sea).

Updated parameters

Biomass (B): The initial biomass input for this group (0.0169 t km^{-2}) was calculated from 2012 bottom trawl survey. This estimate was insufficient to match predator demands, therefore biomass was top-down balanced (EE = 0.8) producing a biomass estimate of 0.5997 t km^{-2}.

Food habits (DC): The diet composition of large-mouth sculpins was determined from stomach samples collected during the 2012 bottom trawl survey (Table 4). The functional group diet is an average diet weighted by biomass. Their diet (by weight) consists of 24% miscellaneous shallow fish, 21% Other sculpins, 14% other crabs, 13% shrimps, 9% eelpouts, 8% snow crab, 7% benthic amphipods, 1% variegated snailfish and 1% polychaetes. Other prey groups of lesser importance (<1%) are other snailfish, miscellaneous crustaceans, other zooplankton, and brittle stars.

Parameters from W13

The P/B of 0.4 used here is unchanged from the preliminary model. In the absence of large-mouth sculpin life history data, this P/B is a general default that approximates other groundfish species (Aydin et al. 2007). The Q/B used here is unchanged from the preliminary model. The Q/B of 2 is a general default value that approximates other groundfish species (Aydin et al. 2007).

Other sculpins

The Other sculpins functional group includes all Cottids not included in the large-mouth sculpin group, including the threaded sculpin (*Gymnocanthus pistilliger*), Arctic staghorn sculpin (*G. tricuspis*), hamecon (*Artediellus scaber*), ribbed sculpin (*Triglops pingeli*), belligerent sculpin (*Megalocottus platycephalus*), leister sculpin (*Enophrys lucasi*), antlered sculpin (*E. diceraus*), and spatulate sculpin (*Icelus spatula*). Additionally, this group includes at least two species from the family Hemitripteridae (sailfin sculpins), the eyeshade sculpin (*Nautichthys pribilovius*) and the crested sculpin (*Blepsias bilobus*).

Updated parameters

Biomass (B): The trawl survey-derived biomass input of 0.0123 t km^{-2} was insufficient to meet predator demands. We therefore used a top-down balance approach (EE = 0.8) which resulted in a biomass estimate of 0.8553 t km^{-2}.

Production (P/B): The estimate of P/B for Other sculpins has changed slightly from the preliminary model. The functional group P/B is an average P/B, weighted by biomass. P/B was re-calculated following the same methods as in the preliminary model, except the biomass weights form the 2012 survey are now used. The P/B has changed from 0.4611 to 0.4593.

Consumption (Q/B): Q/B is also weighted by biomass and it too has been recalculated, also following the same methods as in the preliminary model. Q/B has also modestly decreased from 2.4281 to 2.4152.

Food habits (DC): The diet of Other sculpins was derived from the contents of stomachs collected during the 2012 bottom trawl survey (Table 4). The final functional group diet is an average diet weighted by biomass. The primary prey items (by % weight) are benthic amphipods (48%), polychaetes (24%), anemones (6%), worms etc. (6%), other crabs (6%), pelagic forage fish (4%), and other zooplankton (3%). Other prey groups accounting for `1% or less of the diet composition include, shrimps, miscellaneous crustaceans, brittle stars, snails, bivalves, and snow crabs.

Eelpouts

The eelpouts functional group represents at least 6 species from the family Zoarcidae; marbled eelpout (*Lycodes raridens*), wattled eelpout (*L. palearis*), saddled eelpout (*L. mucosus*), Canadian eelpout (*L. polaris*), polar eelpout (*L. turneri*), and halfbarred eelpout (*Gymnelus hemifasciatus*).

Updated parameters

Biomass (B): The initial biomass input of 0.0168 t km^{-2} for eelpouts was determined from the catch of the 2012 bottom trawl survey. However, this estimate was not adequate to support predator demand and instead a top-down balance was performed (EE = 0.8) producing a biomass estimate of 0.3822 t km^{-2}.

Food habits (DC): Eelpout diet composition was determined through the analysis of eelpout stomachs collected during the 2012 bottom trawl survey. The functional group diet is the average of the individual species diets, weighted by biomass. The primary prey items (by % weight) are polychaetes (54%), benthic amphipods (28%), miscellaneous shallow fish (8%), large-mouth sculpins (5%), other zooplankton (3%), and shrimps (1.5%). Other prey present in trace amounts include other crabs, miscellaneous crustaceans, Other sculpins, variegated snailfish, other snailfish, bivalves, and copepods.

Parameters from W13

The P/B of eelpouts is unchanged from the preliminary model. In the absence of sufficient eelpout life history data, a P/B estimate of 0.4 was used in the preliminary model, which closely approximated the P/B values of other demersal groundfish (Aydin et al. 2007). The eelpout Q/B of 2.0 is also unchanged from the preliminary model. The data required to calculate Q/B for species in this group are not available, and this estimate of Q/B is a general value that approximates the Q/Bs of other groundfish (Aydin et al. 2007).

Pelagic forage fish

The pelagic forage fish group includes four species from three families: Pacific herring (*Clupea pallasi*) from Clupeidae, capelin (*Mallotus villosus*) and rainbow smelt (*Osmerus mordax*) from Osmeridae, and Pacific sand lance (*Ammodytes hexapterus*) from Ammodytidae.

Updated parameters

Biomass (B): The initial biomass input was calculated from the catch data of the 2012 bottom trawl survey (0.0976 t km^{-2}). This initial estimate was not adequate to match the trophic demands from predators and instead a top-down balance was performed (EE = 0.8). This produced a biomass estimate of 1.1906 t km^{-2}.

Production (P/B): Our estimate of P/B for pelagic forage fish is an average P/B, weighted by biomass. In the preliminary -model, P/B was weighted by biomass estimates from the 1990 bottom trawl survey. We have re-calculated P/B here following the same methods; however, we use biomass estimates from the 2012 survey as weights. P/B has decreased from 0.551 to 0.543.

Consumption (Q/B): Q/B is also weighted by biomass, and similarly, Q/B in the preliminary model was weighted by biomass from the 1990 trawl survey. We have recalculated here following the same procedure, but instead use the biomass estimates from the 2012 survey, resulting in a Q/B of 2.92.

Food habits (DC): The pelagic forage fish diet composition was determined through analysis of stomachs collected during the 2012 trawl surveys (Table 4). The diet composition for the functional group is an average of the individual species diet compositions, weighted by biomass. The dominant prey items are other zooplankton (46%), copepods (31%), and miscellaneous shallow fish (19%). Prey types of lesser importance include benthic amphipods, shrimps, large-mouth sculpin, Other sculpins, polychaetes, miscellaneous crustaceans, and other crabs.

Miscellaneous shallow fish

Miscellaneous shallow fish is a composite group of demersal fishes from several families, including poachers (Agonidae), wolfish (Anarhichadidae), lumpsuckers (Cyclopteridae), greenlings (Hexagrammidae), and pricklebacks (Stichaeidae).

Updated parameters

Biomass (B): Our initial biomass estimate of 0.0042 t km^{-2} was calculated from the catch data of the 2012 bottom trawl survey. This estimate was too low to meet predator demands during initial model balancing (i.e., EE > 1). Instead we top-down balanced biomass and calculated a biomass estimate of 6.4984 t km^{-2}. This estimate is more than three orders of magnitude greater than the trawl survey-derived estimate and gives this functional group the highest biomass of all the fish groups. Many species in this group are not efficiently caught with trawl survey gear and the disparity between the top-down forced biomass estimate and the survey-derived estimate in part reflects this. Additionally, miscellaneous shallow fish are a very common prey group (especially Stichaeids) for other fishes of the Chukchi Sea and the top-down estimate reflects this demand from predator groups.

Food habits (DC): The diet composition of the miscellaneous shallow fishes was determined from analysis of stomachs collected during the 2012 bottom trawl survey of the eastern Chukchi Sea (Table 4). The final diet for the functional group is an average of the individual species diets, for those species for which we have diet information, weighted by biomass. The functional group diet composition (by % weight) consists of benthic amphipods (52%), polychaetes (13%), other zooplankton (10%), miscellaneous crustaceans (8%), shrimps (8%), bivalves (5%), and copepods (2%). Prey of lesser importance (1% or less) include worms etc., other crabs, and snails.

Parameters from W13

The estimated P/B of 0.4 is the same as in the preliminary model. The data required to calculate P/B are not available for species in this group, and this estimate is a general value that closely approximates other demersal groundfish (Aydin et al. 2007). The Q/B of miscellaneous shallow fish is unchanged from the preliminary model and remains at 2.0. This is a general value that closely approximates the Q/B of other demersal groundfish (Aydin et al. 2007)

Other snailfish

This functional group is represented primarily by two species from the family Liparidae, the kelp snailfish (*Liparis tunicatus*) and the festive snailfish (*L. marmaratus*). Also present in the catch of the 2012 Arctic Eis survey was the gelatinous seasnail (*L. fabricii*) and several other snailfish identified only as *Liparis* sp. The variegated snailfish (*Liparis gibbus*) is not included in this group and instead makes up its own single-species functional group, primarily due to its distinct diet composition (see below).

Updated parameters

Biomass (B): The initial input for biomass of other snailfish was 0.00225 t km^{-2}. This density estimate was calculated from the catch data of the 2012 Arctic Eis bottom-trawl survey. This initial input for biomass was insufficient to balance the model and a top-down balance was performed with EE = 0.8. This resulted in a density estimate of 0.1351 t km^{-2}.

Production (P/B): There is little to no information regarding life history or vital rates for the species in this functional group. In the absence of species- or region-specific information we assume a P/B of 0.4. This is equivalent to the P/B and Q/B of the miscellaneous shallow fish and variegated snailfish functional groups, and additionally is roughly equivalent to values for taxonomically similar functional groups in previously published models of the Gulf of Alaska, Aleutian Islands, eastern Bering Sea (Trites et al. 1999, Aydin et al. 2007), and northern California Current (Field et al. 2006).

Consumption (Q/B): Species-specific information adequate to support calculation of Q/B for this functional group is presently unavailable. In lieu of species-specific information we assume a Q/B of 2.0. This is equal to the Q/B for the miscellaneous shallow fish and variegated snailfish groups, and is also equivalent to generic values used for taxonomically similar functional groups in published Ecopath models of other northeastern Pacific large marine ecosystems (Trites et al. 1999, Field et al. 2006, Aydin et al. 2007)

Food habits (DC): Other snailfish diet composition was determined from kelp snailfish and festive snailfish stomachs collected during the 2012 bottom trawl survey (Table 4). The functional group diet is an average of these two diets, weighted by biomass. The primary prey items (by % weight) in the other snailfish diet are benthic amphipods (50%), polychaetes (15%), shrimps (10%), pelagic forage fish (7%), variegated snailfish (6%), other crabs (3%), small-mouth flatfish (3%), large-mouth sculpin (2%), Other sculpins (1%), snow crabs (1%), and other zooplankton (1%). Prey items of lesser importance (<1%) include miscellaneous crustaceans, bivalves, and copepods.

Variegated snailfish

Variegated snailfish (*Liparis gibbus*) were included in the miscellaneous shallow fish functional group in W13. Information on the diet of variegated snailfish within the Chukchi Sea was previously unavailable and the assumed miscellaneous shallow fish diet was dominated by amphipods, shrimps, crabs, and polychaetes. During the 2012 Arctic Eis bottom trawl survey, 54 variegated snailfish stomachs were collected and their contents analyzed in the lab. From those stomachs, 58% of their diet was found to consist of fish, and about 33% were fishes from their same functional group, miscellaneous shallow fish. Keeping variegated snailfish and their new diet in the miscellaneous shallow fish group introduced a cannibalistic loop which created computational problems when attempting to balance the model. Therefore, we removed variegated snailfish from miscellaneous shallow fish and now treat them as a single species functional group.

Updated parameters

Biomass (B): A biomass density estimate of 0.0073 t km^{-2} was calculated for variegated snailfish from the catch data of the 2012 Arctic Eis bottom-trawl survey, but was insufficient to balance the model (EE > 1). Instead, a top-down balance was performed with EE of 0.8, producing a density estimate of 0.0987 t km^{-2}.

Production (P/B): Because there is little to no life history information for this species, we assume the same P/B as the miscellaneous shallow fish group, which formerly included the variegated snailfish. In lieu of a species-specific estimate, the P/B is assumed to be 0.4. This value is a default assumption used for taxonomically similar functional groups in previous Ecopath models of large marine ecosystems in Alaska. Trites et al. (1999) used a P/B of 0.4 for several demersal fish groups of the eastern Bering Sea and Aydin et al. (2007) used a P/B of 0.4 for their miscellaneous shallow fish group (including snailfish) in models of the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska.

Consumption (Q/B): There is no information available to support the calculation of Q/B for this species and therefore we assume the same Q/B as the miscellaneous shallow fish group, which formerly included variegated snailfish. The Q/B is assumed be to 2.0. This value is a default assumption used for taxonomically similar functional groups in previous Ecopath models of large marine ecosystems in Alaska. Aydin et al. (2007) used a Q/B of 2.0 for their miscellaneous shallow fish group (including snailfish) in models of the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska.

Food habits (DC): The diet composition for this group was determined through the analysis of variegated snailfish stomachs collected in the eastern Chukchi Sea during the 2012 bottom trawl survey (Table 4). The diet consists of shrimps (29%), miscellaneous shallow fish (18%), other snailfish (14%), Other sculpins (11%), large-mouth sculpin (8%), benthic amphipods (7%), pelagic forage fish (3%), polychaetes (3%), large-mouth flatfish (1%), other zooplankton (1%), Arctic cod (1%), snow crab (1%), and eelpouts (1%). Other prey groups accounting for less than 1% of the diet include other crabs, bivalves, miscellaneous crustaceans, worms etc., and copepods.

Alaska skate

A single adult (95 cm total length) Alaska skate (*Bathyraja parmifera*) was caught in the southern Chukchi Sea during the 2012 Arctic Eis bottom trawl survey (Goddard et al. 2014). Beach cast specimens have previously been found in 2010 near Pt. Hope and Kivalina in the southern Chukchi Sea (Mecklenburg et al. 2011). Additionally, several Alaska skates were caught throughout the northern Bering Sea during 2010 NOAA summer bottom trawl survey (Lauth 2011). In consideration of these recent observations of Alaska skate we have decided to add them to our Ecopath model as a single species functional group.

Updated parameters

Biomass (B): The biomass density of 0.00537 t km^{-2} for Alaska skates was calculated from the catch data of the 2012 Arctic Eis bottom trawl survey. There are no known predators of Alaska skate in the Chukchi Sea and their EE is 0.0.

Production (P/B): Frisk et al. (2001) compiled life-history parameters for elasmobranch fishes over a wide geographic range and estimated the potential rate of population increase for medium-sized elasmobranchs (100-200cm) as 0.21. Aydin et al. (2007) used the medium-sized elasmobranch estimate of Frisk et al. (2001) as a proxy for the P/B ratio of Alaska skates in the eastern Bering Sea and assigned them a P/B of 0.20. Matta and Gunderson (2007) used three different published methods to indirectly estimate the natural mortality (M) of Alaska skate in the eastern Bering Sea and found M to range from 0.14 to 0.28. Here we use the midpoint (M = 0.21) of the natural mortality rate range provided by Matta and Gunderson (2007) as a proxy for Z, the instantaneous mortality rate of Alaska skate in the eastern Chukchi Sea. Under steady-state conditions P/B is approximated by Z (Allen 1971) and we use P/B = 0.21 for Alaska skate.

Consumption (Q/B): Sufficient information to estimate Q/B is not presently available for Alaska skates. In previous models of other Alaska ecosystems (eastern Bering Sea, Aleutian Islands, and Gulf of Alaska), Aydin et al. (2007) estimated Q/B by assuming a growth efficiency (GE) that was intermediate between sharks and large predatory fishes (e.g., Pacific halibut). They assumed a growth efficiency of 0.1 which produced a Q/B of 2.0. In lieu of adequate information, we make the same assumption here with a GE of 0.1 which resulted in a Q/B of 2.1.

Food habits (DC): The diet composition of skates in the eastern Chukchi Sea is unknown at this time. In the absence of region-specific data, the diet of Alaska skates was derived from stomach data collected in the eastern Bering Sea by scientists from the Resource Ecology and Ecosystem Modeling (REEM) program at the NOAA Alaska Fisheries Science Center in Seattle. The diet compositions were acquired by querying the REEM food habits database (a detailed description of the database can be found at http://www.afsc.noaa.gov/REFM/REEM/Data/Default.htm) with their Diet Analysis Tool (Lang 2004). We limited our diet queries to survey strata in the northern half of the surveyed area and inshore of the continental slope (NMFS survey strata 20, 41, 42, and 43, station depth generally less than 100 m, see Figure 2 in Lauth (2011)). These strata experience seasonal ice coverage and are regularly encompassed by the eastern Bering Sea “cold pool” (see Figure 6 in Lauth (2011)) which creates cool summer demersal conditions (Wyllie-Echeverria and Wooster 1998, Mueter and Litzow 2008, Stabeno et al. 2012, Stevenson and Lauth 2012). Though the precise conditions and extent of the cold pool vary from year to year and are not equal to the Chukchi Sea, we assumed Alaska skate diet information collected from here was a better approximation of their diet in the Chukchi Sea than to import diet information from more distant ecosystems or from different species.

Alaska skate diet composition is described from stomachs collected in the eastern Bering Sea (n = 1,773 non-empty stomachs). The primary prey items (by % weight) of Alaska skate are Arctic cod (27%), snow crab (26%), shrimps (11%), small-mouth flatfish (6%), other crabs (6%), pelagic forage fish (5%), eelpouts (4%), benthic amphipods (3%), large-mouth flatfish (3%), large-mouth sculpins (2%), salmon returning

(2%), miscellaneous shallow fish (2%), polychaetes (1%), and other zooplankton (1%). Other prey items of lesser importance (<1%) include variegated snailfish, other snailfish, Pacific cod, Other sculpins, benthic urochordate, miscellaneous crustaceans, urchins-dollars-cucumbers, cephalopods, snails, bivalves, anemones, brittle stars, and copepods.

Walleye pollock

Walleye pollock (*Gadus chalcogrammus*) are a dominant component of the ecosystem in the adjacent eastern Bering Sea, and there they support one of the world's largest single-species fisheries (Ianelli et al. 2013, Zador 2013). Due to their commercial importance and ecological significance in the eastern Bering Sea they are treated as a single-species in this Ecopath model.

Updated parameters

Biomass (B): Walleye pollock biomass is estimated to be 0.00054 t km^{-2} from the catch data of the 2012 Arctic Eis bottom trawl survey. They experience little predation mortality in the Chukchi Sea and a top-down balance was not necessary.

Production (P/B): The data required to estimate P/B for walleye pollock in the Chukchi Sea is not presently available. Sufficient data does exist for walleye pollock in the eastern Bering Sea where this species is intensively studied, however, walleye pollock in the eastern Chukchi Sea experience considerably different growing conditions (e.g., temperature) and have only been observed at much smaller sizes (16 cm or less in the present study, Goddard et al. (2014)). In lieu of region-specific data, we apply the region-specific estimates of P/B for another gadid, Arctic cod (*Boreogadus saida*), to walleye pollock. Arctic cod are found at similar sizes to walleye pollock in the eastern Chukchi Sea, both species can be found in demersal and pelagic environments, and both are known to feed on zooplankton. Given the taxonomic relationship between Arctic cod and walleye pollock, and in consideration of ecological similarities between these two species, we felt the Arctic cod P/B was our best approximation of walleye pollock P/B in the eastern Chukchi Sea. We use the Arctic cod P/B of 0.8690 for walleye pollock.

Consumption (Q/B): The data required to calculate Q/B for walleye pollock in the eastern Chukchi Sea is not presently available. Instead we apply the region-specific Q/B of 3.008 calculated for Arctic cod to walleye pollock.

Food habits (DC): The diet composition of walleye pollock was determined from stomach specimens collected during the 2012 Arctic Eis bottom trawl survey (Table 4). The primary prey items were fish, in particular 6.5% Arctic cod and 47.2% Teleostei. In the absence of information to guide how to best attribute the teleost portion of the diet to our functional groups, we have attributed it to the only identified fish prey, Arctic cod. This increases the Arctic cod portion of the walleye pollock diet to 53.7%, but this is likely an overestimate. Because walleye pollock have such a small presence in the Chukchi Sea, they account for less than 0.1% of Arctic cod predation mortality, despite Arctic cod accounting for more than half of their diet. The rest of the diet consists of copepods (15%), shrimps (14%), other zooplankton (10%), benthic amphipods (4%), and miscellaneous crustaceans (3%).

Pacific cod

Pacific cod (*Gadus macrocephalus*) is a predatory groundfish present in low abundance in the Chukchi Sea, but far more abundant and commercially important in other more southerly parts of their range in Alaska, such as the Bering Sea.

Updated parameters

Biomass (B): Pacific cod are present in very low abundance in the eastern Chukchi Sea; only four were caught during the 2012 bottom trawl survey (Goddard et al. 2014). From that catch data, their biomass is estimated to be $3.79*10^{-5}$ t km^{-2}. Pacific cod are subject to very little predation mortality in the Chukchi Sea and have an EE of 0.744.

Production (P/B): The information required to calculate P/B for Pacific cod in the Chukchi Sea is not presently available. Based on taxonomic relation and presumed similarities in diet and habitat requirements, we apply the region-specific estimate of P/B = 0.5477 calculated for saffron cod to Pacific cod.

Consumption (Q/B): Sufficient information is not presently available to support region-specific calculations of Q/B for Pacific cod. In lieu of this information, we use the region-specific estimate of Q/B for saffron cod instead. Pacific cod are assigned a Q/B of 2.8028.

Parameters from W13

Only one Pacific cod stomach was collected during the 2012 Arctic Eis bottom trawl survey and that was not an adequate sample size to define a new diet for this species. The one stomach contained two prey types, shrimp (81% by weight) and polychaetes (19%). Diet composition (DC) is unchanged from the preliminary model. The major prey groups are shrimps (29%), Arctic cod (16%), snow crab (15%), benthic amphipods (14%), polychaetes (7%), miscellaneous shallow fish (6%), other zooplankton (5%), and other crabs (5%).

Saffron cod

Saffron cod (*Eleginus gracilis*) is a demersal gadid typically found in shallow, nearshore waters of Alaska (Wolotira 1985).

Updated parameters

Biomass (B): Our initial biomass input for saffron cod of 0.1080 t km^{-2}, was derived from the catch data of the 2012 Arctic Eis bottom trawl survey. This estimate was insufficient to meet predator demands (EE > 1) during initial attempts to balance the model and a top-down balance was performed instead. This produced a biomass estimate of 0.9791 t km^{-2}.

Production (P/B): Under the assumption of equilibrium conditions, P/B is equal to Z, the instantaneous natural mortality rate (Allen 1971). Following this assumption, we use the regression estimator of mortality of Hewitt and Hoenig (2005) to approximate P/B. This method requires only an estimate of maximum age. We acquired a preliminary maximum age estimate of 8 (Helser et al. In press) derived from specimens collected during the Arctic Eis trawl surveys. This produced an estimated P/B of 0.5477.

Consumption (Q/B): We calculated Q/B following the methods of Aydin (2004) which requires only an estimate of mortality (Z) and an estimate of the growth parameter *k* from the von Bertalanffy growth function (vBGF). We used our estimate of Z from the aforementioned P/B calculation and used a preliminary estimate of the vBGF k parameter for saffron cod from Helser et al. (In press) . This resulted in a Q/B estimate of 2.8028.

Food habits (DC): The diet composition of saffron cod was determined from stomachs collected during the 2012 Arctic Eis bottom trawl survey (Table 4). The primary prey items (by % weight) of saffron cod are shrimps (48%), miscellaneous shallow fish (35%), worms etc. (6%), benthic amphipods (4%), other zooplankton (4%), and polychaetes (3%). Prey items present in trace amounts (<1%) include miscellaneous crustaceans, snails, other crabs, and copepods.

Arctic cod

Arctic cod (*Boreogadus saida*) is one of the more ubiquitous groundfish species in the eastern Chukchi Sea and can be found in demersal and pelagic environments as well as in association with sea ice during ice-covered periods (Bradstreet et al. 1986, Gradinger and Bluhm 2004, Geoffroy et al. 2011, Parker-Stetter et al. 2011, Renaud et al. 2012).

Updated parameters

Biomass (B): The initial input for Arctic cod biomass (0.1460 t km^{-2}) was calculated from the 2012 Arctic Eis bottom trawl survey. This estimate was insufficient to match demands from predators, and a top-down balance (EE = 0.8) was performed instead. This resulted in a biomass estimate of 1.0449 t km^{-2}.

Production (P/B): Under the assumption of equilibrium conditions, P/B is equal to Z, the instantaneous natural mortality rate (Allen 1971). Following this assumption, we use the regression estimator of mortality of Hewitt and Hoenig (2005) to approximate P/B. This method requires only an estimate of maximum age. We acquired a preliminary maximum age estimate of 5 (Helser et al. In press) derived from specimens collected during the Arctic Eis trawl surveys. This produced an estimated P/B of 0.8690.

Consumption (Q/B): We calculated Q/B following the methods of Aydin (2004) which requires only an estimate of mortality (Z) and an estimate of the growth parameter *k* from the von Bertalanffy growth function (vBGF). We used our estimate of Z from the aforementioned P/B calculation and used a preliminary estimate of the vBGF k parameter for Arctic cod from Helser et al. (In press). This resulted in a Q/B estimate of 3.008.

Food habits (DC): We determined the diet composition of Arctic cod from stomachs collected during the 2012 Arctic Eis trawl surveys. The primary prey items (by % weight) of Arctic cod include copepods (37%), other zooplankton (28%), shrimps (16%), benthic amphipods (10%), pelagic forage fish (5%), and miscellaneous crustaceans (1%). Other prey groups of lesser importance (<1%) include Arctic cod, polychaetes, large-mouth sculpin, large-mouth flatfish, eelpouts, snailfish, miscellaneous shallow fish, other crabs, and bivalves.

Salmon outgoing

The salmon outgoing functional group includes at least five species of anadromous Pacific salmon: pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), sockeye salmon (*O. nerka*), and Chinook salmon (*O. tshawytscha*) (Alverson and Wilimovsky 1966, Smith et al. 1966). Salmon are present in the ecosystem in two distinct pulses, the outgoing smolts leaving streams for the ocean, and the adults returning to spawn in the streams. The salmon outgoing group represents the out-migrating smolts leaving streams for the ocean.

Updated parameters

None

Parameters from W13

The biomass and abundance of outgoing salmon smolts in the Chukchi Sea are not known with precision. The biomass estimate (B) used here is unchanged from the preliminary model. In the absence of suitable data to calculate abundance or biomass estimates, the biomass of outgoing salmon was assumed to be 1/10 of the returning salmon biomass, for a density estimate of $5.21 * 10^{-4}$ t km^{-2}. In lieu of a region-specific estimate of P/B, the P/B of 1.28 for salmon outgoing is taken from a taxonomically similar functional group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). A Q/B of 13.56 is used for outgoing salmon and is unchanged from the preliminary model. Lacking a region-specific estimate of Q/B, this estimate is taken from a taxonomically similar functional group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The diet composition (DC) we use for outgoing salmon is unchanged from the preliminary model. The diet compositions of juvenile pink and chum salmon in the northern Bering and eastern Chukchi seas is dominated by zooplankton, including copepods (Moss et al. 2009), and the diet used here is divided evenly between these two groups.

Salmon returning

The salmon returning functional group includes at least five species of anadromous Pacific salmon: pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), sockeye salmon (*O. nerka*), and Chinook salmon (*O. tshawytscha*) (Alverson and Wilimovsky 1966, Smith et al. 1966). Salmon are present in the ecosystem in two distinct pulses, the outgoing smolts leaving streams for the ocean, and the adults returning to spawn in the streams. The salmon returning group represents the adult salmon returning from the ocean to spawn in streams.

Updated parameters

None

Parameters from W13

The salmon returning biomass estimate (B) of 0.00521 t km^{-2} is unchanged from the preliminary model. There are few estimates of abundance for returning salmon in the eastern Chukchi Sea (e.g., Smith et al. 1966). In their place, catch records (Booth and Zeller 2008, Eggers et al. 2010) were used as a best, conservative indication of abundance and were used to derive the density estimate. The salmon returning P/B of 1.65 is taken from a taxonomically similar functional group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The Q/B of 11.6 for salmon returning is also unchanged from W13, and similarly, is taken from a taxonomically similar functional group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). Diet (DC) descriptions for juvenile pink and chum salmon in the northern Bering and eastern Chukchi seas indicate their diet is dominated by zooplankton, including copepods (Moss et al. 2009). The diet of salmon in the Bering Sea is also dominated by zooplankton (Davis et al. 2009). The diet composition used here is divided evenly between copepods and other zooplankton.

Benthic Invertebrates

Cephalopods

The cephalopods group is assumed to consist of only octopods. Recently, two unidentified squid (Order Teuthoidea) were caught within the Chukchi Sea and weighed a combined 12 g (Weems 2014). However, at this time observations of squid in the Chukchi Sea are very limited and therefore, they are not formally included in this functional group. Historically, octopods have been recorded throughout the eastern Chukchi Sea (Sparks and Pereyra 1966, Feder and Jewett 1978). Recent records of octopods in the Chukchi Sea have primarily been for *Benthoctopus sibiricus* (Blanchard et al. 2013a, Goddard et al. 2014). Previous records from the northeastern Chukchi Sea have also included *Benthoctopus leioderma* (Feder et al. 1994a).

Updated parameters

Biomass (B): Octopods were not present in the 2012 beam trawl catch data and were scarcely represented in the catch from the 2012 bottom trawl survey (Goddard et al. 2014). Octopods are not well sampled with bottom trawling gear and producing reliable biomass estimates from survey data in the nearby eastern Bering Sea has proven problematic (Conners and Conrath 2010). We calculated an estimated biomass of $6.5 * 10^{-4}$ t km^{-2} from the Arctic Eis bottom trawl data and used that as an initial biomass input. However, this estimate was insufficient to meet predator demands and a top-down balance was performed (EE = 0.8) resulting in a biomass estimate of 0.011 t km^{-2}.

Parameters from W13

The cephalopod P/B of 1.77 is unchanged from the preliminary model and is a molluscan mean P/B from Cusson and Bourget (2005). Cephalopod Q/B of 8.85 was estimated by assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. 1999). The cephalopod diet composition (DC) is the same as the diet used in the preliminary model. Octopods in Alaska are known to consume crabs, bivalves, and snails (Vincent et al. 1998). Lacking region-specific and species-specific information, the cephalopod diet composition is divided evenly between bivalves, snails, snow crabs, and other crabs.

Bivalves

The bivalves group is represented by numerous species from at least 13 families of the Class Bivalvia, including clams, mussels, cockles, scallops, and scaphopods. Bivalves are a dominant part of the eastern Chukchi Sea benthic community in abundance and biomass (Feder et al. 2007, Schonberg et al. 2014).

Updated parameters

Biomass (B): Many bivalves burrow into the sediment and are not well sampled by trawling gear. To calculate biomass we instead use data from quantitative benthic grab samples collected with van Veen grabs (0.1 m^{-2}) at sampling stations across the eastern Chukchi Sea (Feder et al. 1994b, Feder et al. 2007). We calculated a biomass estimate of 90.288 t km^{-2}.

Production (P/B): The bivalve P/B (1.3) from the preliminary model was taken from taxonomically equivalent groups in Ecopath models of other Alaska ecosystems (data pedigree = 6, Aydin et al. 2007). This estimate was derived from a from a single study conducted on the coast of Sweden (Evans 1984). Expanding our literature search we identified eight P/B estimates for five bivalve species known to occur in the Chukchi Sea, taken from six different studies (Table 8). None of these studies used specimens collected within the Chukchi Sea, but the calculated P/B estimates were for species known to occur in the Chukchi Sea. These species-specific estimates were seen as an improvement over the previous P/B estimate and are used here in place of the P/B used in the previous model. The P/Bs are averaged producing a functional group P/B of 0.756. The data pedigree for this new P/B is 5 (species-specific estimates).

Table 8. -- Bivalve P/B values used in the calculation of the bivalve group P/B. *Genus now changed to *Astarte*.

Reference	Taxa	P/B	Region
Asmus (1987)	*Mya arenaria*	0.41	North Sea
Burke and Mann (1974)	*Mya arenaria*	2.54	Nova Scotia
Gagayev (1990)	**Nicania montagui*	1.74	East Siberian Sea
Gagayev (1990)	**Tridonta borealis*	0.55	East Siberian Sea
Petersen (1978)	*Serripes groenlandicus*	0.13	Greenland
Petersen (1978)	*Serripes groenlandicus*	0.1	Greenland
Sejr et al. (2002)	*Hiatella arctica*	0.095	Greenland
Warwick and Price (1975)	*Mya arenaria*	0.48	England

Consumption (Q/B): Q/B is solved for by Ecopath with an assumed GE of 0.2. The updated estimate of P/B in combination with GE = 0.2 results in a Q/B of 3.78.

Parameters from W13

Bivalves are assumed to be primarily benthic detritivores and may also feed on suspended particles and small phytoplankton (Ruppert and Barnes 1994). Their diet (DC) is divided between benthic microbes (25%) and benthic detritus (75%).

Snails

The snail functional group includes all gastropods (including nudibranchs) found in the eastern Chukchi Sea, except for pteropods, which are included in other zooplankton. Numerous gastropod species are present in the eastern Chukchi Sea, representing at least 17 families (Blanchard et al. 2013b).

Updated parameters

Biomass (B): The snail functional group is dominated by Buccinids in terms of biomass, which account for more than 70% of the snail biomass caught with beam trawl gear during the 2012 Arctic Eis survey. Of secondary importance are the Naticids, who represent more than 19% of the snail biomass caught in beam trawls. We calculated a biomass density estimate of 1.384 t km^{-2} from the Arctic Eis beam trawl catch data, and used this as our biomass input.

Production (P/B): The snail P/B (1.81) used by W13 was derived from a single study conducted in the intertidal zone of the North Sea (Asmus 1987). That P/B was neither region-specific nor species-specific. Lacking region-specific or species-specific estimates of P/B we instead use a molluscan mean P/B of 1.77 (±0.14, n = 230) (Cusson and Bourget 2005).

Consumption (Q/B): Ecopath solves for Q/B with an assumed GE of 0.2. The updated P/B estimate of 1.77 in combination with the assumed GE results in a Q/B of 8.85.

Food habits (DC): The snail diet used in the preliminary model was based on general diet descriptions presented in Feder and Jewett (1981). Lacking more specific diet data, the estimated snail diet in W13 was spread evenly amongst possible prey groups. We improve upon this diet here by incorporating information from snail diet studies conducted in Alaska (Shimek 1984), Russia (Kosyan 2007), and the north Atlantic (Taylor 1978). The Buccinid diet at high latitudes is generally dominated by bivalves and polychaetes (Taylor 1978, Shimek 1984). Other prey items of lesser importance include barnacles, amphipods, sipunculans, priapulans, and carrion (detritus) (Taylor 1978, Shimek 1984, Kosyan 2007). Naticids specialize in feeding on bivalves by boring holes through their shells (Kabat 1990). Based on dietary descriptions from a variety of sources the snail diet used here consists of bivalves (50%), polychaetes (30%), amphipods (5%), worms etc. (5%), miscellaneous crustaceans (5%), and benthic detritus (5%).

Snow crab

Snow crab (*Chionoecetes opilio*) are a commercially important species of crab in the nearby eastern Bering Sea (NPFMC 2011) and are considered a species of potential commercial importance within the Arctic management area (NPFMC 2009, Wilson and Ormseth 2009). Tanner crabs (*C. bairdi*) are also sometimes referred to as snow crabs, but they are not included here as their range does not extend north into the Chukchi Sea. Snow crabs in the eastern Chukchi Sea are generally smaller than those found in the eastern Bering Sea, and rarely grow to commercially legal size (carapace width ≥ 78 mm). During the 2012 Arctic Eis bottom trawl survey, only 29 of the ~28,000 snow crab caught were legal sized males (Goddard et al. 2014).

Updated parameters

Biomass (B): We calculated a snow crab biomass estimate of 3.170 t km^{-2} from the Arctic Eis beam trawl catch data.

Parameters from W13

Snow crab P/B of 1.0 was derived from stock assessment data specific to the eastern Bering Sea stock by Trites et al. (1999), Aydin et al. (2002), and Aydin et al. (2007). The Q/B estimate of 2.75 is also unchanged from the preliminary model, and was previously derived by Trites et al. (1999), Aydin et al. (2002), and Aydin et al. (2007).

The diet composition (DC) of snow crabs in Alaska is not well known. Previous food web models of large marine ecosystems in Alaska (Aydin et al. 2002, Aydin et al. 2007, W13) have based the diet composition of snow crabs (*Chionoecetes opilio* and *C. bairdi*) on the work of Tarverdieva (1981) who reported on the diet of *C. opilio* and *C. bairdi* in the eastern Bering Sea. Identification of snow crab stomach contents is hampered by the grinding of prey in the gastric mill, which reduces prey to a mushy pulp and limits the quantification of snow crab diet composition. The mastication of prey precludes the use of other common methods for quantifying stomach contents (Hyslop 1980), such as percent number (%N) or percent weight (%W). Divine et al. (In press) have been working toward addressing this data gap by examining the stomach contents of snow crabs (*C. opilio*) collected in the Chukchi and Beaufort seas. They have compiled a list of prey taxa they found in the stomachs of snow crabs and reported the frequency that these items occurred in stomachs (% frequency of occurrence [FO]). Some of the most frequently occurring prey categories across their study region were the polychaete *Cistenides hyperborean* (59.5%), bivalves (57.1%), and other polychaetes (42.9%). Other prey groups that were less frequently observed included amphipods (27.2%), decapods (25.7%), brittle stars (22.2%), and fishes (7.4%). Among the decapod prey, Divine et al. (In press) frequently observed brachyuran crabs, which they note could possibly have been snow crabs. Detritus, sediment, and various bits of otherwise taxonomically unidentifiable prey (e.g., bits of shells or fleshes, crustacean exoskeleton) were also commonly observed among stomach contents. Similarly, Feder and Jewett (1978) examined the stomach contents of snow crabs collected in Norton Sound and also found sediment (56% FO), detritus (22.5% FO), and unidentified material (18.0%) to be among the most frequently occurring prey categories.

Our Ecopath modeling framework requires predator diet compositions to be expressed in terms of percent weight (or volume). It is not possible to accurately translate diet data described in terms of %FO to %W or volumetric composition. %FO can provide a qualitative view of observed prey items, but gives no indication of volumetric or numerical importance (Hyslop 1980). %FO may also be positively biased for prey with hard, indigestible parts (e.g., shells, exoskeletons) that linger in the digestive tract for longer periods of time, and be negatively biased for softer prey items (e.g., worms, mollusk flesh) that are digested and evacuated quickly. In consideration of the limitations of %FO diet data, we do not use the %FO values provided in Divine et al. (In press) and continue to use the snow crab diet composition previously described by Tarverdieva (1981) and summarized by Aydin et al. (2007). The major prey groups are polychaetes (27%), benthic detritus (27%), bivalves (21%), brittle stars (6%), and benthic amphipods (6%). Other prey of lesser importance include other crabs, snails, worms etc., miscellaneous crustaceans, the urchins-dollars-cucumbers group, other zooplankton, phytoplankton, sponge, sea stars, and anemones.

Other crabs

The other crabs group includes all anomuran and brachyuran crabs with the exception of snow crab (*C. opilio*). Other brachyurans caught during the 2012 Arctic Eis trawl surveys included the circumboreal toad crab (*Hyas coarctatus*) and helmet crab (*Telmessus cheiragonus*). Anomurans caught during the Arctic Eis surveys included several species of hermit crabs (Paguridae) and two species of king crab; red king crab (*Paralithodes camtschaticus*) and blue king crab (*P. platypus*).

Updated parameters

Biomass (B): We calculated a biomass estimate of 3.067 t km^{-2} from the 2012 Arctic Eis beam trawl catch data.

Parameters from W13

The other crabs P/B of 0.82 was taken from Ecopath models of the western and eastern Bering Sea (Aydin et al. 2002, Aydin et al. 2007). The Q/B of 4.10 was calculated with an assumed growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. 1999). The other crabs diet composition (DC) is based on the diets of taxonomically similar functional groups in the eastern Bering Sea Ecopath model (Aydin et al. 2007), and is divided equally among bivalves, polychaetes, worms etc., and benthic detritus.

Shrimps

The shrimp functional group includes all decapod shrimps occurring in the eastern Chukchi Sea. Shrimps are represented in the trawl survey data by multiple species from the families Crangonidae, Hippolytidae, and Pandalidae (Goddard et al. 2014).

Updated parameters

Biomass (B): Shrimp are not well sampled with the trawling gear, and biomass estimates calculated from the catch data are assumed to underestimate the actual biomass. Initial attempts to balance the model with a biomass estimate of 1.655 t km^{-2}, calculated from the Arctic Eis beam trawl data, proved to be insufficient to meet predator demands (EE > 1). A top-down balance was performed instead resulting in a biomass estimate of 7.4922 t km^{-2}.

Parameters from W13

The shrimp P/B of 0.58 and Q/B of 2.41 are unchanged from W13 and are from taxonomically similar functional groups in Ecopath models of other large marine ecosystems in Alaska (Aydin et al. 2007). The diet composition (DC) of shrimps is the same as that used in the preliminary model. Lacking region-specific information, the diet composition in the preliminary model was based on diet descriptions found in multiple studies (Rice et al. 1980, Feder and Jewett 1981, Feder et al. 1981, Rice 1981). The estimated diet consists of benthic detritus (40%), bivalves (15%), benthic amphipods (15%), polychaetes (15%), and miscellaneous crustaceans (15%).

Sea stars

The sea star functional group is represented by several species from the families Solasteridae, Goniopectinidae, Echinasteridae, Asteriidae, and Pterasteridae, all belonging to the Class Asteroidea.

Updated parameters

Biomass (B): We calculated a sea star biomass estimate of 2.180 t km^{-2} from the 2012 Arctic Eis beam-trawl catch data.

Production (P/B): The P/B used for sea stars in the preliminary model (P/B = 1.21) was borrowed from Ecopath models of other Alaska ecosystems and was derived from a minimum amount of information (Aydin et al. 2007). That P/B estimate was neither region-specific nor species-specific. Lacking P/B estimates of taxonomic and geographic relevance to our study region, we instead use an Echinoderm mean P/B of 0.34 (±0.06, n = 28) calculated by Cusson and Bourget (2005).

Consumption (Q/B): Q/B is calculated by Ecopath with an assumed GE of 0.2. The updated P/B estimate in combination with the assumed GE results in a Q/B of 1.70.

Parameters from W13

The diet composition (DC) of sea stars is unchanged from the preliminary model. The diet was derived from information from multiple studies (Feder and Jewett 1978, Feder and Jewett 1981) and consists of bivalves (52%), sand dollars (27%), polychaetes (13%), snails (5%), and benthic urochordates (3%).

Brittle stars

Species from the order Ophiurida comprise the brittle star functional group. They are represented in the 2012 Arctic Eis trawl survey catch data by species from four genera, *Amphiophiura, Ophiura, Ophiacantha, and Ophiopholis*.

Updated parameters

Biomass (B): We calculated a biomass estimate of 5.644 t km^{-2} for brittle stars from quantitative benthic grab samples collected with van Veen grabs (0.1 m^{-2}) from sampling locations across the eastern Chukchi Sea (Feder et al. 1994b, Feder et al. 2007).

Production (P/B): Previously, brittle stars were assigned a P/B of 1.21 in W13. This estimate was neither species-specific nor region-specific. It was taken from Ecopath models of other Alaska ecosystems and was derived from a minimum of information (Aydin et al. 2007). P/B estimates for species known to occur in the Chukchi Sea are unavailable at the time of this writing. We have identified 5 P/B estimates for brittle star species belonging to genera that are known to occur in the Chukchi Sea, *Ophiocten* and *Ophiura* (Table 9). A P/B range of 0.43 to 0.54 was calculated by Gage (2003) for *Ophiocten gracilis* along the Scottish continental slope in the NE Atlantic Ocean. Dahm (1993) estimated P/B ratios of 0.32 for *Ophiura albida* and 0.43 for *Ophiura ophiura* at locations on the German Bight in the southeastern North Sea. A P/B of 0.69 was calculated by Warwick et al. (1978) for *O. ophiura* in Carmarthen Bay, Wales. Similarly, a P/B of 0.5 was estimated for *O. ophiura* in Bristol Channel, Wales, by Warwick and George (1980) (cited by Dahm 1993). In lieu of P/B estimates specific to our study region and taxa, we calculate a mean P/B from the aforementioned sources. We use the midpoint of the range (0.485) reported by Gage (2003) and the four other point estimates to calculate a mean P/B of 0.485.

Table 9. -- Brittle star P/B values used to calculate the brittle star group P/B. †Midpoint of range reported by Gage (2003). *Cited by Dahm (1993).

Reference	Species	P/B	Region
Gage (2003)	*Ophiocten gracilis*	†0.485	NE Atlantic Ocean
Dahm (1993)	*Ophiura albida*	0.32	North Sea
Dahm (1993)	*Ophiura ophiura*	0.43	North Sea
Warwick et al. (1978)	*Ophiura ophiura*	0.69	Wales
Warwick and George (1980)*	*Ophiura ophiura*	0.5	Wales

Consumption (Q/B): Q/B is calculated by Ecopath with GE set at 0.2. The updated estimate of P/B in combination with GE results in Q/B = 2.43.

Parameters from W13

The brittle star diet composition (DC) is unchanged from the preliminary model. In the absence of region-specific information, the diet composition was based on information from multiple sources (Warner 1982, Harris et al. 2009). The diet consists of 50% benthic detritus, with the remaining 50% divided evenly among bivalves, benthic amphipods, polychaetes, and miscellaneous crustaceans.

Basket stars

Basket stars of the eastern Chukchi Sea are represented by a single species, *Gorgonocephalus eucnemis* of the family Gorgonocephalidae. They are among the most abundant trawl-caught invertebrates in the eastern Chukchi Sea by weight (Goddard et al. 2014).

Updated parameters

Biomass (B): Basket star biomass was estimated from the 2012 Arctic Eis beam trawl catch data as 0.5099 t km^{-2}.

Production (P/B): In the preliminary food web model, basket stars were assigned a P/B of 1.21 which was borrowed from Ecopath models of other Alaska ecosystems (Aydin et al. 2007). This P/B estimate was a general proxy and was neither species-specific nor region-specific. Lacking a P/B estimate specific to our study region or taxa, we use an Echinoderm mean P/B of 0.34 (±0.06, n = 28) calculated by Cusson and Bourget (2005).

Consumption (Q/B): The Q/B of 1.70 is calculated by Ecopath with an assumed GE of 0.2.

Parameters from W13

The basket star diet composition (DC) is unchanged from the preliminary model. In lieu of region-specific diet data, the basket star diet was derived using information from multiple sources (Patent 1970, Warner 1982, Emson et al. 1991, Rosenberg et al. 2005). The diet consists of equal parts benthic amphipods, miscellaneous crustaceans, copepods, and other zooplankton.

Urchins, dollars, cucumbers

The urchins, dollars, cucumbers functional group combines echinoderms from three orders: Clypeasteroida (sand dollars), Dendrochirotida (sea cucumbers), and Echinoida (sea urchins). It is primarily represented in the eastern Chukchi Sea by the green sea urchin (*Strongylocentrotus droebachiensis*), the common sand dollar (*Echinarachnius parma*), and sea cucumbers of the genera *Psolus* and *Cucumaria*.

Updated parameters

Biomass (B): We estimated the biomass of urchins, dollars, cucumbers to be 36.2897 t km^{-2} from quantitative benthic grab samples collected with van Veen grabs (0.1 m^{-2}) at sampling locations across the eastern Chukchi Sea (Feder et al. 1994b, Feder et al. 2007). Larger organisms, such as the green sea urchin and common sand dollar, may not have been well sampled with the benthic grabs.

Production (P/B): The group consisting of sea urchins, sand dollars, and sea cucumbers was assigned a P/B of 0.61in W13. This P/B was borrowed from Ecopath models of other Alaska ecosystems (Aydin et al. 2007) and was not specific the Chukchi Sea. We have expanded our literature search and identified 5 species-specific P/B estimates (Table 10), including 3 estimates from high latitude regions surrounding Greenland (Blicher et al. 2007, Blicher et al. 2009). Four of the P/B estimates are for the sea urchin *Strongylocentrotus droebachiensis*, and one for the sand dollar, *Echinarachnius parma*. We have averaged these five P/B estimates together to arrive at a group P/B of 0.695.

Table 10. -- P/B estimates from the literature used to calculate P/B for the urchins, dollars, cucumbers functional group.

Reference	Taxa	P/B	Location
Miller and Mann (1973)	*Strongylocentrotus droebachiensis*	0.8	NW Atlantic, Canada
Blicher et al. (2007)	*S. droebachiensis*	0.29	NE Greenland
Blicher et al. (2009)	*S. droebachiensis*	0.31	SW Greenland
Blicher et al. (2009)	*S. droebachiensis*	0.37	SW Greenland
Steimle (1990)	*Echinarachnius parma*	1.705	NW Atlantic, USA

Consumption (Q/B): The Q/B of 3.48 is calculated by Ecopath with the updated P/B estimate and an assumed GE of 0.2.

Parameters from W13

The diet composition (DC) of urchins, dollars, cucumbers is not changed from the preliminary model. Quantitative diet descriptions were not available for this group and the diet was based on generalized diet descriptions (DeRiddler and Lawrence 1982, Massin 1982, Ables 2000). The diet consists of benthic detritus (75%) and phytoplankton (25%).

Sponge

The sponge functional group contains all taxa from the Phylum Porifera. Sponge are frequently damaged when caught with trawling gear and are often identified only as Porifera in survey catch data (Wolotira et al. 1977, Barber et al. 1994). Recently, the black papilate sponge (*Halichondria sitiens*) was found to be one of the dominant benthic invertebrates (by weight) caught during the 2012 Arctic Eis bottom trawl survey of the eastern Chukchi Sea (Goddard et al. 2014).

Updated parameters

Biomass (B): We calculated a sponge biomass estimate of 0.527 t km^{-2} from the 2012 Arctic Eis beam trawl catch.

Parameters from W13

Sponge P/B is unchanged from the preliminary model and remains at 1.0 (Aydin et al. 2007). The sponge Q/B is also unchanged and remains at 5.0, which was calculated assuming a growth efficiency of 0.2. The diet composition (DC) of sponges is not changed from the preliminary model, and consists of benthic microbes (25%) and benthic detritus (75%).

Benthic urochordate

Tunicates from the Class Ascidiacea comprise the benthic urochordate group. In the eastern Chukchi Sea, they are represented by species from at least four families: Pyuridae, Corellidae, Styelidae, and Didemnidae (Blanchard et al. 2013a). During the 2012 Arctic Eis bottom trawl survey of the eastern Chukchi Sea, Ascidians were found to be among the dominant benthic invertebrates (by weight), including *Boltenia ovifera*, the sea potato (*Styela rustica*), and the sea peach (*Halocynthia aurantium*) (Goddard et al. 2014).

Updated parameters

Biomass (B): We estimated the biomass of benthic urochordates from the 2012 Arctic Eis beam trawl catch data as 1.160 t km^{-2}.

Parameters from W13

We did not change benthic urochordate P/B from W13 and it remains at 3.58 (Asmus 1987). The Q/B of 17.9 is also unchanged from the preliminary model, and was calculated assuming a growth efficiency of 0.2. The diet composition (DC) of this group has not changed from the preliminary model. They are filter feeders (Abbott 1966, Ruppert and Barnes 1994)and their diet consists of benthic bacteria (25%) and benthic detritus (75%).

Anemones

The anemones functional group consists of Cnidarians from the Order Actinaria. In the eastern Chukchi Sea they are primarily represented by the mottled anemone (*Urticina crassicornis*) and species from the genus *Stomphia* (Blanchard et al. 2013a, Goddard et al. 2014).

Updated parameters

Biomass (B): We estimated anemone biomass from the 2012 Arctic Eis beam trawl catch as 0.384 t km^{-2}.

Parameters from W13

P/B is unchanged from W13 and remains at 1.0. This P/B is from a taxonomically similar functional group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The Q/B has also not changed and remains at 5.0, which was calculated with an assumed growth efficiency of 0.2. The food habits of anemones in Alaska are not well known and the diet composition (DC) is based on anemone diet descriptions from other regions (Frank and Bleakney 1978, Dalby 1992, Kruger and Griffiths 1998). The diet composition is divided evenly between benthic amphipods, miscellaneous crustaceans, bivalves, benthic microbes, and benthic detritus.

Corals

Cnidarians from the Order Alcyonacea (soft corals) comprise the corals functional group. In the eastern Chukchi Sea they are primarily represented by species of the genus *Gersemia* (Blanchard et al. 2013a, Goddard et al. 2014, Schonberg et al. 2014).

Updated parameters

Biomass (B): We estimated coral biomass to be 0.026 t km^{-2} from the 2012 Arctic Eis beam trawl catch.

Parameters from W13

P/B has not been changed from the preliminary model and remains at 0.05. This P/B is from a taxonomically similar functional group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The corals Q/B of 0.23 was calculated with an assumed growth efficiency of 0.2. The diet composition

(DC) of corals has not changed from the preliminary model, and consists of benthic microbes (25%) and benthic detritus (75%).

Benthic Amphipods

The benthic amphipods functional group includes species from the crustacean suborders Gammaridea and Caprellidea. Amphipods are found throughout the eastern Chukchi Sea and are an important prey item for gray whales that migrate to the Chukchi Sea to feed during summer (Highsmith and Coyle 1992).

Updated parameters

Biomass (B): Our initial biomass estimate of 8.074 t km^{-2} was calculated from the benthic grab data collected with van Veen grabs (0.1 m^{-2}) (Feder et al. 1994b, Feder et al. 2007), but was insufficient to balance the model (EE > 1). Instead we performed a top-down balance which resulted in an estimated biomass of 20.526 t km^{-2}.

Parameters from W13

The P/B of benthic amphipods has not changed from the preliminary model and remains at 1.0 (Highsmith and Coyle 1992). Q/B has also not changed from W13 and stays at 5.0, which was calculated with an assumed growth efficiency of 0.2. Benthic amphipod diet composition (DC) is the same as in W13. They are assumed to primarily be detritivores (Thomson 1986) and their diet is divided evenly between benthic microbes and benthic detritus.

Polychaetes

Polychaete worms are a dominant component of the eastern Chukchi Sea benthic community in terms of abundance and biomass (Feder et al. 2007, Blanchard et al. 2013b, Schonberg et al. 2014). The polychaete assemblage in the eastern Chukchi Sea is diverse as well, with over 100 species known to occur there (Blanchard et al. 2013b, Schonberg et al. 2014).

Updated parameters

Biomass (B): The biomass of polychaetes was estimated at 27.808 t km^{-2} from the benthic grab data collected with van Veen grabs (0.1 m^{-2}) at sampling stations spread across the eastern Chukchi Sea (Feder et al. 1994b, Feder et al. 2007).

Table 11. -- Polychaete P/B values used in the calculation of the Polychaete group P/B. †Reported as *Harmothoe sarsi* by Asmus (1987). *Reported as *Tharyx marioni* by Asmus (1987) and Warwick et al. (1978).

Reference	Species	P/B	Region
Asmus (1987)	*Ampharete acutifrons*	2.23	Wadden Sea, intertidal (North Sea)
Asmus (1987)	*Capitella caitata*	3.78	Wadden Sea, intertidal (North Sea)
Asmus (1987)	*Eteone longa*	4.67	Wadden Sea, intertidal (North Sea)
Asmus (1987)	†*Bylgides sarsi*	1.14	Wadden Sea, intertidal (North Sea)
Asmus (1987)	*Heteromastus filiformis*	2.75	Wadden Sea, intertidal (North Sea)
Asmus (1987)	*Scoloplos armiger*	2.99	Wadden Sea, intertidal (North Sea)
Asmus (1987)	**Aphelochaeta marioni*	5.99	Wadden Sea, intertidal (North Sea)
McLusky and McIntyre (1988)	*Ampharete acutifrons*	4.58	Long Is., subtidal
McLusky and McIntyre (1988)	*Chaetozone setosa*	1.28	England, offshore 80m
McLusky and McIntyre (1988)	*Heteromastus filiformis*	1.01	England, offshore 80m
McLusky and McIntyre (1988)	*Lumbrineris fragilis*	1.34	England, offshore 80m
Valderhaug (1985)	*Lumbrineris fragilis*	0.826	Oslofjord, Norway
Warwick and Price (1975)	*Ampharete acutifrons*	5.5	England (intertidal estuary)
Warwick et al. (1978)	*Spiophanes bombyx*	4.86	Carmarthen Bay, S. Wales
Warwick et al. (1978)	**Aphelochaeta marioni*	0.79	Carmarthen Bay, S. Wales

Production (P/B): The P/B used for polychaetes (P/B = 1.645) in W13 was an average based on multiple polychaete P/B values presented in McLusky and McIntyre (1988). There are several published estimates of P/B for polychaetes (e.g., Cusson and Bourget 2005), none of which are specific to our study region. Estimates of polychaete P/B are also available from other Ecopath models. Trites et al. (1999) use a P/B of 1.37 for a composite functional group including polychaetes in their model of the eastern Bering Sea. In a similar composite benthic group, (Field 2004) used a P/B of 2.5 in a model of the northern California Current. Harvey et al. (2010) use a P/B of 4.4 for polychaetes in their model of Puget Sound, Washington, USA. Pedersen et al. (2008) used P/Bs of 0.5 and 0.75 for composite functional groups which included polychaetes in their model of a Norwegian fjord. A P/B of 2.97 was used for polychaetes in models of the eastern Bering Sea, Gulf of Alaska, and Aleutian Islands by Aydin et al. (2007) and in the western Bering Sea by Aydin et al. (2002). Cusson and Bourget (2005) calculated a mean P/B for all Annelida as 3.37 (±0.38, n = 120). In our search of the literature we identified 15 P/B estimates for polychaete species known to occur in the eastern Chukchi Sea (Table 11); however, none of the estimates are specific to our study region. We have averaged these 15 P/B estimates to arrive at a functional group P/B of 2.916.

Consumption (Q/B): Q/B is calculated by Ecopath with an assumed GE of 0.2. In combination with the updated P/B estimate this results in Q/B = 14.58.

Parameters from W13

The diet composition (DC) of polychaetes is unchanged from the preliminary model. They are assumed to primarily be detritivores and their diet is divided evenly between benthic microbes and benthic detritus.

Worms, etc.

Worms etc. is a composite group that consists of several invertebrate taxa including the phyla Sipuncula, Echiura, Priapula, Nemertea, Brachiopoda, and Bryozoa; and additionally the annelid Subclass Hirudinea (leeches) and the cnidarian Class Hydrozoa (hydroids).

Updated parameters

Biomass (B): We estimate the biomass of worms etc. to be 17.039 t km^{-2} from the benthic grab data collected with van Veen grabs (0.1 m^{-2}) at sampling stations spread across the eastern Chukchi Sea (Feder et al. 1994b, Feder et al. 2007).

Parameters from W13

The worms etc. P/B of 2.23 was taken from taxonomically equivalent groups in Ecopath models of the Bering Sea (Aydin et al. 2002). The Q/B of 11.15 was solved with an assumed growth efficiency of 0.2. The worms etc. diet composition (DC) has not changed from the preliminary model. They are assumed to primarily be detritivores and their diet is evenly divided between benthic microbes and benthic detritus.

Miscellaneous crustaceans

The miscellaneous crustaceans group combines all the remaining benthic-oriented crustaceans that are not already included in a functional group. This group includes isopods, cumaceans, barnacles, pycnogonids, and ostracods.

Updated parameters

Biomass (B): We calculated the miscellaneous crustaceans biomass to be 5.581 t km^{-2} from the benthic grab data collected with van Veen grabs (0.1 m^{-2}) at sampling stations spread across the eastern Chukchi Sea (Feder et al. 1994b, Feder et al. 2007).

Production (P/B): In the preliminary model, the miscellaneous crustaceans group had a P/B of 3.83. That estimate was derived from multiple P/B estimates that were not specific to the Chukchi Sea and included P/B estimates for several species not known to occur within our study region. We have improved upon that estimate here and calculate a mean P/B from published P/B estimates for species known to occur within the eastern Chukchi Sea (Table 12). Asmus (1987) calculated a P/B of 1.11 for the barnacle, *Balanus crenatus*, in the North Sea. Persson (1989) studied the life cycle and productivity of the cumacean, *Diastylis rathkei*, in the southern Baltic Sea and calculated a mean P/B of 2.03. Rachor et al. (1982) also studied the productivity of *D. rathkei* in the southern Baltic in Kiel Bay, and in the German Bight of the North Sea, where they calculated P/B ratios of 2.7 and 3.2, respectively. Ansell et al. (1978) reported a P/B estimate of 1.0 for *D. rathkei*. Lacking P/B estimates specific to our study region, we use a mean P/B of 2.008 calculated from the aforementioned P/B estimates.

Table 12. -- P/B values used in the calculation of the functional group P/B for Miscellaneous crustaceans.

Reference	Taxa	P/B	Region
Asmus (1987)	*Balanus crenatus*	1.11	North Sea
Persson (1989)	*Diastylis rathkei*	2.03	Southern Baltic Sea
Rachor et al. (1982)	*D. rathkei*	3.2	North Sea
Rachor et al. (1982)	*D. rathkei*	2.7	Southern Baltic Sea
Ansell et al. (1978)	*D. rathkei*	1	Temporate/northern boreal

Consumption (Q/B): Q/B is calculated by Ecopath with an assumed GE of 0.2. In combination with the estimated P/B of 2.008, this results in an estimated Q/B of 10.04.

Parameters from W13

The diet composition (DC) of miscellaneous crustaceans has not been changed from the preliminary model. They are assumed to primarily be detritivores and their diet is divided evenly between benthic microbes and benthic detritus.

Pelagic Invertebrates and Microbes

Jellyfish

The jellyfish group includes all Scyphozoan jellies found in the eastern Chukchi Sea and is primarily represented by the sunrise jellyfish (*Chrysaora melanaster*) (Goddard et al. 2014).

Updated parameters

Biomass (B): We calculated a biomass estimate of 0.372 t km^{-2} from the 2012 Arctic Eis bottom trawl survey.

Parameters from W13

We did not change the jellyfish P/B from the preliminary model, and it remains 0.88. This P/B was taken from a taxonomically equivalent functional group in a Bering Sea Ecopath model (Aydin et al. 2007). The jellyfish Q/B of 3.0 was estimated by Aydin et al. (2007) from summer ration information reported by Brodeur et al. (2002) for an equivalent jellyfish group in a Bering Sea Ecopath model. The jellyfish diet composition (DC) is unchanged from W13 and they are assumed to feed on pelagic prey. Their assumed diet consists of copepods (67.5%), other zooplankton (22.5%), pelagic microbes (5%), and phytoplankton (5%).

Copepods

Copepods are a dominant component of the pelagic ecosystem in the Chukchi Sea in terms of biomass and abundance (Ashjian et al. 2003, Hopcroft et al. 2010, Matsuno et al. 2011, Eisner et al. 2013, Questel et al. 2013). They are an important node in the Chukchi Sea food web, connecting pelagic and sympagic primary production to higher trophic level predators, including larger zooplankton (Båmstedt and Karlson 1998, Brodeur and Terazaki 1999, Dalpadado et al. 2008), fish (Gray et al. 2015, Whitehouse et al. In press), seabirds (Springer and Roseneau 1985), and marine mammals (Moore et al. 2010). Many of the copepod species found in the Chukchi Sea are of Pacific origin and have been advected into the Chukchi Sea through the Bering Strait (Springer et al. 1989), though the species composition and geographic distribution is known to vary annually (Pinchuk and Eisner In press).

Updated parameters

Biomass (B): Biomass is not input to the model and instead we used a top-down balance, assuming EE = 0.8, to estimate copepod biomass as 2.04 t km^{-2}. Copepod biomass was also top-down balanced in the preliminary model, also with EE = 0.8.

Parameters from W13

We did not change copepod P/B from W13 and continue to use the P/B of 6.0, which was taken from a taxonomically equivalent group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). We also continue to use the Q/B of 27.74 for copepods from W13, which was taken from a taxonomically equivalent group in the eastern Bering Sea Ecopath model (Aydin et al. 2007). We did not change the diet composition (DC) of copepods from the diet used in the preliminary model. Arctic copepods are generally omnivorous, consuming both phytoplankton and microzooplankton (Conover et al. 1986, Runge and Ingram 1988, 1991, Levinsen et al. 2000, Campbell et al. 2009). The specific composition of copepod diets within the Chukchi Sea is not well known, and the assumed diet used here is evenly split between pelagic microbes (microzooplankton) and phytoplankton.

Other zooplankton

The other zooplankton group consists of all other meso- and macro-zooplankton species excluding copepods. This group includes euphausiids, mysids, hyperiids, larvaceans, pteropods, chaetognaths, meroplankton, and ctenophores. Similar to copepods, many of the species in the other zooplankton group are of Pacific origin and have been advected into the Chukchi Sea through the Bering Strait (Springer et al. 1989, Hopcroft et al. 2010).

Updated parameters

Biomass (B): As in the preliminary model, we did not input biomass to the model and instead biomass is estimated by Ecopath, with EE set to 0.8. This produced a biomass estimate of 1.225 t km^{-2}.

Parameters from W13

P/B is not changed from the preliminary model and remains at 5.48. This P/B was originally calculated for euphausiids in the southeastern Bering Sea (Smith 1991), and is used for taxonomically similar functional groups in the eastern Bering Sea Ecopath model (Aydin et al. 2007). The Q/B of 15.64 is also unchanged from the preliminary model, and was solved for with an assumed growth efficiency of 0.35 (Aydin et al. 2007). We did not change the diet composition (DC) of other zooplankton from the diet used in the preliminary model. Diet studies of related taxa in other ecosystems indicates that species from this group may feed on phytoplankton, copepods, other zooplankton, and pelagic microbes (Båmstedt and Karlson 1998, Brodeur and Terazaki 1999, Acuña et al. 2002, Dalpadado et al. 2008). Lacking region-specific diet data, the diet for other zooplankton is based on the estimated diet of taxonomically similar functional groups from the eastern Bering Sea Ecopath model (Aydin et al. 2007), and consists of phytoplankton (60%), copepods (25%), and pelagic microbes (15%).

Pelagic microbes

The pelagic microbes (microzooplankton) group is a composite group that primarily consists of bacteria and protozoans, and is intended to represent processes in the pelagic microbial loop.

Updated parameters

Biomass (B): Biomass estimates of pelagic microbes in the eastern Chukchi Sea are not available. A top-down balance, with EE = 0.8, was used in the preliminary model and we use the same approach here. The top-down biomass estimate of pelagic microbes is 1.49 t km^{-2}.

Parameters from W13

We did not change the pelagic microbe P/B and continue to use the P/B of 26.25 from W13. This P/B was derived from information in Kirchman et al. (2007) on growth rates for bacteria and the total prokaryotic community in shelf areas (<100 m) of the western Arctic Ocean. Q/B remains at 75.0, which was estimated with an assumed growth efficiency of 0.35 (Aydin et al. 2007). We did not change the diet composition (DC) of pelagic microbes from the diet in the preliminary model. Pelagic microbes are assumed to consume primarily phytoplankton and pelagic detritus (Sherr et al. 2009). Their assumed diet consists of 70% phytoplankton and 30% pelagic detritus.

Benthic microbes

The benthic microbes group is a composite group that primarily consists of bacteria and protozoans, and is intended to represent processes in the benthic microbial loop.

Updated parameters

Biomass (B): The biomass of benthic microbes on the eastern Chukchi Sea shelf is not well known, so a top-down balance with EE = 0.8 was used in the preliminary model and we use the same approach here. This resulted in a density estimate of 22.31 t km^{-2}.

Parameters from W13

The P/B for benthic microbes is assumed to be similar to that of pelagic microbes so they are given the same P/B of 26.25. Q/B is assumed to be the same for benthic microbes as for pelagic microbes, and is solved for with an assumed growth efficiency of 0.35 (Aydin et al. 2007). The diet (DC) of benthic microbes is not changed from the preliminary model. Their diet is assumed to consist of 100% benthic detritus.

Phytoplankton

Phytoplankton is a composite group combining all primary producers in the eastern Chukchi Sea. The dominant component of the autotrophic phytoplankton biomass in the Chukchi Sea is diatoms and they also rank second in terms of abundance (Sukhanova et al. 2009).

Primary production in the Chukchi Sea is seasonally limited by light (e.g., day length, low sunlight angle) and sea ice cover. During winter the low levels of light in combination with the presence of sea ice prevent phytoplankton blooms from initiating. As day length increases during spring, the snow cover begins to melt and primary production begins with an ice algae bloom within the sea ice (Cota et al. 1991, Horner et al. 1992). As the sea ice continues to melt and break up under increasing amounts of sunlight, the water column becomes stratified with low-density meltwater at the surface helping create conditions favorable for development of an ice-edge bloom (Alexander and Niebauer 1981, Sakshaug and Skjoldal 1989, Perrette et al. 2011). The ice-edge bloom then follows the receding ice edge northward.

During the open-water season in the Chukchi Sea, primary production is highest near the ice edge and in the open water of the southern Chukchi Sea where primary production is fueled by the input of nutrient-rich water from the Bering Sea (Hansell et al. 1993, Wang et al. 2005). In general, ice algae is thought to account only for a small portion of total primary production on seasonally ice-covered Arctic shelves and most of the primary production is thought to come from phytoplankton production in open waters and near the ice edge (Subba Rao and Platt 1984, Gosselin et al. 1997, Hill and Cota 2005, Pabi et al. 2008). Recent field studies in the Chukchi Sea have recorded the presence of prolific phytoplankton blooms in the water column beneath fully consolidated sea ice (Arrigo et al. 2014). Under-ice production is not detected by satellite-based methods used for estimating primary production and if such under ice blooms occur regularly, satellite-based estimates may underestimate total production on Arctic shelves (Arrigo et al. 2012). Lowry et al. (2014) re-analyzed the satellite record back to 1998, attempting to identify evidence of under-ice phytoplankton blooms, and found evidence suggesting that such under-ice blooms may be widespread in the Chukchi Sea. It is not yet known whether under-ice blooms in the Chukchi Sea are something that has only recently begun to occur or whether they have been a regular feature for many years but have gone undetected (Arrigo et al. 2014).

Primary production is spatially variable in the eastern Chukchi Sea and generally ranges from about 20 to > 400 g C $m^{-2}yr^{-1}$ (Sakshaug 2004). Parrish (1987) estimated primary production to range from ~50 g C $m^{-2}yr^{-1}$ in the northeastern Chukchi Sea to ~150 g C $m^{-2}yr^{-1}$ over the southern Chukchi Sea. Similarly, Hill and Cota (2005) estimated primary production to be 70.5 g C $m^{-2}yr^{-1}$ over the northeastern Chukchi Sea continental shelf. Portions of the southern Chukchi Sea that are supplied with nutrient-rich water flowing in from the Bering Sea may experience much higher levels of productivity. Springer and McRoy (1993) described such a location in the south-central Chukchi Sea, which had an estimated annual production of 470 g C $m^{-2}yr^{-1}$, and may range as high as 720 g C $m^{-2}yr^{-1}$.

Updated parameters

Biomass (B): Phytoplankton biomass was initially top-down balanced with EE set to 0.8, which resulted in a low biomass estimate of ~2.4 t km^{-2}. If we assume that C weight is 45% of dry weight and that dry weight is 15% of wet weight (Valiela 1995), that's approximately 0.16 g C m^{-2}. Assuming a 150 day growing season and our P/B of 75, this is equivalent to ~12 g C $m^{-2}yr^{-1}$, which is lower than most estimates of primary production in the eastern Chukchi Sea. This low top-down estimate is primarily due to the relatively low grazing pressure from zooplankton (Campbell et al. 2009, Sherr et al. 2009). A side effect of this low phytoplankton biomass estimate is that benthic detritus was out of balance (EE > 1). This is the result of heavy trophic pressure on benthic detritus by abundant benthic invertebrates (See Detritus section below). In this model phytoplankton is the largest contributor to benthic detritus. This same situation, with benthic detritus being out of balance, occurred during efforts to balance the preliminary model. To bring benthic detritus back into balance, W13 increased the biomass of phytoplankton in increments of 1 t km^{-2} until benthic detritus became balanced (EE ≤ 1). The resulting combination of B and P/B was equivalent to ~170 g C $m^{-2}yr^{-1}$ (Whitehouse et al. 2014). We elected to use the same approach here and increased phytoplankton biomass in increments of 0.1 t km^{-2} until benthic detritus came back into balance. This resulted in a biomass estimate of 27.8 t km^{-2}. In combination with P/B = 75 and assuming a 150 day growing season, this is equivalent to an annual production of ~141 g C m^{-2}.

Parameters from W13

Phytoplankton P/B is unchanged from the preliminary model and remains 75. This P/B was derived from an average maximum daily growth rate of 0.5 d^{-1} for Arctic diatoms in the Barents Sea (Gilstad and Sakshaug 1990), scaled up to an annual rate.

Detritus

During our initial attempts to balance the model, benthic detritus was out of balance (EE > 1). This was the result of high trophic demand for detritus in combination with insufficient supply to the benthic detrital pool. Within the model, the primary source to the benthic detrital pool is phytoplankton. In the eastern Chukchi Sea much of the phytoplankton bloom and ice algae experience low grazing pressure by zooplankton and ultimately sink out of the water column and are incorporated into the benthic detrital pool. Additionally, phytoplankton and detritus may be advected into the Chukchi Sea from the northern Bering Sea through Bering Strait (Stoker 1981, Hansell et al. 1989, Springer and McRoy 1993, Feder et al. 1994b, Dunton et al. 2005, Carmack and Wassmann 2006). Such outside production may represent a significant portion of the total annual phytoplankton production in the Chukchi Sea. Using a nitrogen budget, Hansell and Goering (1990) estimated that approximately 60% of the annual primary productivity in the highly productive northern Bering Sea (just south of the Bering Strait) is advected into the southern Chukchi Sea where it eventually settles to the benthos. Additionally, other detrital matter, such as phytodetritus, detritus of terrestrial origin, marine snow, and zooplankton fecal pellets, may be advected into the southern Chukchi Sea from the northern Bering Sea (Walsh et al. 1997). The downward flux and horizontal distance that detrital matter may travel before deposition to the benthos is affected by the sinking rate, the horizontal velocity, water column depth, and grazing by zooplankton (Turner 2002). The sinking rate of such detrital matter is influenced by particle size, particle aggregation potential, particle fragmentation, the presence of or colonization by microbes, and for fecal pellets, the predator diet (Turner 2002). In the area of the Bering Strait there is reduced deposition of organic matter to the benthos, as reflected by lower sediment oxygen uptake rates (Grebmeier and McRoy 1989), which may be due to increased current velocities while transiting the narrow Bering Strait (Coachman et al. 1975, Clement et al. 2005, Woodgate et al. 2005). The suspended organic content passing through the Bering Strait eventually settles to the benthos in the south-central Chukchi Sea where the current slows at recognized areas of increased sedimentation (Dunton et al. 2005, Grebmeier et al. 2006). The delivery of organic matter to the Chukchi Sea is also affected by interannual and seasonal variation in the flow velocity through Bering Strait. The flow regime through Bering Strait and the subsequent residence time of water parcels within the Chirikov Basin are related to the local wind regime (Coachman et al. 1975, Coachman and Shigaev 1992). During periods when wind conditions reduce flow through the Bering Strait, water parcels and their entrained organic matter may spend increasing amounts of time transiting the Chirikov Basin, increasing the deposition of organic matter south of Bering Strait and reducing the amount of organic matter available for deposition north of Bering Strait (Coachman and Shigaev 1992). Increased velocity and turbulence as water masses pass through Bering Strait mixes the water column, resupplying surface layers with nutrients, setting the stage for another production cycle to begin in the southern Chukchi Sea (Coachman and Shigaev 1992).

The biomass of the benthic community is positively correlated with primary production in the overlying water masses throughout the Chukchi Sea (Grebmeier et al. 1988, Grebmeier 1993, Dunton et al. 2005). Primary production rates are lower in the northeastern Chukchi Sea (Parrish 1987, Springer and McRoy 1993, Hill and Cota 2005) but high benthic biomass is thought to be sustained there by the advection of carbon rich waters from the northern Bering and southern Chukchi seas into the northeastern Chukchi Sea (Feder et al. 1994b). Organic contributions from the Bering Sea to food webs of the Chukchi Sea have been supported by stable isotope analyses (Dunton et al. 1989).

The advection of primary production and other organic matter northward through Bering Strait is an important part of the carbon budget (Walsh et al. 1989, Walsh et al. 1997) and food web of the Chukchi Sea (Dunton et al. 1989, Dunton et al. 2005, Grebmeier et al. 2006). The seasonal and interannual variation of physical, chemical, and biological properties of water masses transiting Bering Strait make it difficult, if not impossible, to know with accuracy the specific contribution that outside primary production and other organic matter make to the eastern Chukchi Sea food web. Lacking the required information to adequately portray these processes in our trophic model, we elect to use the same approach here to balance benthic detritus as that used in the preliminary model. Previously, W13 brought benthic detritus into balance by supplementing the benthic detrital pool with additional phytodetritus by increasing the phytoplankton biomass, and the same approach is used here in this model update (See Phytoplankton above). This approach resulted in a phytoplankton biomass of 27.8 t km^{-2}, which in combination with its P/B of 75, and assuming a 150 day growing season, was equivalent to an annual primary production of ~141 g C m^{-2}.

Model Balancing

There were few adjustments to input parameters required to bring the updated model into balance. This was at least in part due to the present model update beginning with the preliminary model that was already balanced. Many of the updated input parameter values were only modestly different from the pre-existing model parameters, and therefore the new input parameters resulted in minimal change to model outputs (e.g., EE). However, a few significant adjustments were required to achieve a balanced model.

Perhaps the most conspicuous parameter adjustment was the increase in phytoplankton biomass. The initial top-down estimate of phytoplankton biomass was low, and when considered in combination with P/B (i.e., B*(P/B)) was equivalent to a total annual production estimate lower than most published estimates for this region (~12 g C $m^{-2}yr^{-1}$). Additionally, benthic detritus was out of balance (EE > 1). In both the preliminary model and the present model update, phytodetritus is the largest contributor to the benthic detrital pool. To satisfy the estimated detrital demand from consumers and bring benthic detritus back into balance, we supplemented the benthic detrital pool with phytodetritus by increasing phytoplankton biomass. This same tactic for balancing benthic detritus was used to balance the preliminary model (W13). This line of reasoning is consistent with previous studies documenting the strong pelagic-benthic coupling in this ecosystem (e.g., Dunton et al. 2005, Grebmeier 2012, Blanchard et al. 2013b, Blanchard and Feder 2014). The final phytoplankton biomass was equivalent to an annual production rate of ~141 g C m^{-2}, which falls within the range of annual primary production estimates reported in the literature (e.g., Sakshaug 2004).

Another significant adjustment was the reconfiguration of the miscellaneous shallow fish functional group. Previously, this functional group contained a number of lesser-known demersal fish taxa including pricklebacks, snailfish, and poachers, and had a generalized diet based on stomachs collected for some of the same species in the eastern Bering Sea (W13), as opposed to the Chukchi Sea. In this model update we were able to improve the diet description for miscellaneous shallow fish with region-specific diet information (Whitehouse et al. In press). However, this new diet data brought to light the high level of predation between species within this functional group. Some of the species within the miscellaneous shallow fish group were important predators of each other, and that was not the case with the diets used in the preliminary model. Because this group was top-down balanced, cannibalism created a loop that resulted in unreasonably high biomass estimates for several fish functional groups. To eliminate the looping problem introduced by cannibalism, we removed from the miscellaneous shallow fish group those species that were feeding on other species within this functional group, primarily the variegated snailfish and other snailfish species (*Liparis* sp.). We split the miscellaneous shallow fish functional group from W13 into three functional groups: 1) miscellaneous shallow fish, 2) variegated snailfish, and 3) other snailfish. This eliminated the problems associated to within-group cannibalism and reduced the top-down biomass estimates of fish groups to better reflect the true demand of these fish species within the ecosystem.

Biomass was top-down balanced for several of the functional groups for which survey data was available to calculate a biomass estimate. This included 11 of the 16 fish functional groups, cephalopods, and shrimp. The combinations of initial input parameters (e.g., B, P/B, etc.) for these functional groups were insufficient to balance the model (EE > 1). After reviewing all the input parameters for these functional groups and examining related input parameters for predators (e.g., B, Q/B, P/B, DC) of these functional groups, it was determined the most likely cause for imbalance was underestimation of biomass. For the fish functional groups, cephalopods, and shrimp, this is consistent with the findings of Whitehouse et al. (2014), who also top-down balanced these same groups. An underestimation of biomass for fish, cephalopods, and shrimp from the bottom trawl survey data may reflect spatial limitations of survey coverage, patchy species distribution, and interannual variation in abundance, or low catchability of some species to the sampling gear (e.g., mesh size of the bottom-trawl net).

The biomass of benthic amphipods was not top-down balanced in the preliminary model but is top-down balanced in the present model. In this model we used a considerably lower region-specific density estimate (8.1 t km^{-2} vs. 33.9 t km^{-2}) as an initial model input which resulted in insufficient biomass to satisfy the trophic demand for benthic amphipods in the system (i.e., EE > 1). The higher biomass density estimate of 33.9 t km^{-2} used by W13 was taken from an area in the northern Bering Sea known to have high densities of amphipods (Stoker 1981), and may have overestimated the biomass of benthic amphipods in the eastern Chukchi Sea. After re-examining all the input parameters for benthic amphipods and their predators (e.g., B, Q/B, DC), it was determined that underestimation of biomass was the most likely cause for imbalance. Benthic invertebrate groups, including amphipods, have patchy distributions in the Chukchi Sea which may arise from variation in the properties of the overlying water masses (e.g., temperature, salinity), sediment characteristics, and food availability (e.g., delivery of organic nutrients) (Feder et al. 2007, Blanchard et al. 2013b, Blanchard and Feder 2014, Schonberg et al.

2014). Amphipod densities as high as 26 t km^{-2} have been observed at sampling stations in the northeastern Chukchi Sea (Schonberg et al. 2014). The Ecopath top-down biomass estimate of 20.5 t km^{-2} for benthic amphipods is lower than the densities observed in the northern Bering Sea and lower than some of the higher amphipod densities recently observed in eastern Chukchi Sea (e.g., Schonberg et al. 2014).

Model Comparisons

Updated model versus preliminary model

Biomass

The pattern of biomass distribution amongst the broader taxonomic categories is much the same in the updated model as it was in Whitehouse et al. (2014) (Table 13). Benthic-oriented invertebrates account for the majority (76.6%) of the total system biomass (excluding detritus), followed by phytoplankton (9.6%) and microbes (8.2%). All remaining aggregate groups account for 5.6% of total system biomass combined.

Despite the broad similarities between the preliminary model and this model update, there are some significant changes in the biomass estimates for the aggregated groups. In general, biomass estimates increased for the higher trophic level (TL) groups (TL > 3.5): mammals (average TL = 4.4), seabirds (average TL = 4.1), and fishes (average TL = 3.9); and biomass estimates generally decreased for lower trophic level groups: benthic invertebrates (average TL = 2.8), jellyfish (TL = 3.4), microbes (average TL = 2), and phytoplankton (TL = 1). The one exception to this pattern is zooplankton (average TL = 2.5), whose aggregate biomass had a modest increase.

The aggregated biomass of marine mammal groups increased by 10% from the preliminary model to the updated model, due to an increase in the estimated biomass of bowhead whales. The bowhead whale biomass estimate in the preliminary model was based on an estimate of the population size in 1988 (6,928 whales) (George et al. 2004). Bowhead whale biomass in the updated model is based on a more recent abundance estimate for the population in 2004 of 12,631 whales (Koski et al. 2010), which is nearly double the estimate used in the preliminary model. The biomass estimates used for gray whales and Pacific walrus in the updated model are both also based on more recent abundance estimates; however, unlike bowhead whales these changes resulted in a decrease in their respective biomass estimates. The biomass estimates for all other marine mammals are unchanged. The net result is an increase in total marine mammal biomass of ~10%.

Table 13. -- Comparison of the distribution of biomass among aggregated groups and system metrics between the preliminary model of Whitehouse et al. (2014) and the present model update. The proportion of total system biomass (excluding detritus) represented by aggregated functional groups is shown as a percentage. The percent change in the aggregated biomass for each group is shown in the column "% change in B". Similarly, changes in the value of system metrics from the preliminary model to the present model updated are shown in the column "% change in metric".

Aggregate group	This study	Whitehouse et al. (2014)	% change in B
Mammals	0.3%	0.2%	10%
Seabirds	0.0012%	0.0004%	144%
Fish	4.1%	1.1%	215%
Benthic invertebrates	76.6%	81.1%	-23%
Jellyfish	0.1%	0.2%	-43%
Zooplankton	1.1%	0.9%	3%
Microbes	8.2%	7.0%	-4%
Phytoplankton	9.6%	9.6%	-18%
System metric			**% change in metric**
Total system throughput (t km^{-2} yr^{-1})	8,452	10,000	-15%
Total production (P, t km^{-2} yr^{-1})	3,000	3,578	-16%
Total net primary production (t km^{-2} yr^{-1})	2,085	2,550	-18%
Total biomass (B, t km^{-2}, excluding detritus)	291.1	355.5	-18%
Total P/Total B (excluding detritus)	10.3	10.1	2%

There was a substantial increase in seabird biomass of 144%. This increase in seabird biomass is due to the addition of two new seabird functional groups (Procellarids and Scolopacids) representing four species, whose biomass was not included in the preliminary model. The biomass estimates of all other bird species did not change.

Total fish biomass made the largest leap, increasing by 215%. This increase is not due to the new trawl-survey data and new biomass estimates, but rather the new region-specific diet compositions we added showing higher levels of piscivory than previously modeled. As was the case with the preliminary model, survey-derived estimates of fish biomasses were not sufficient to supply the estimated consumption, and top-down balance was required to estimate biomass. For several fishes, the new diet information indicated higher levels of piscivory than was estimated in the preliminary model with diet data for the same species from the nearby eastern Bering Sea. The higher levels of piscivory also necessitated breaking the miscellaneous shallow fish group into three functional groups to eliminate computational problems associated with cannibalism. The additional top-down pressure from other fishes due to the updated information on diet composition was sufficient to substantially increase the total fish biomass.

The aggregated biomass of benthic-oriented invertebrates decreased by 23% from the preliminary model to the updated model. This is primarily due to the inclusion of updated biomass estimates for several benthic invertebrate functional groups in the updated model. In the preliminary model, density estimates for eight of the benthic invertebrate groups were based on average densities reported in Stoker (1981) for the combined continental shelves of the eastern Chukchi and eastern Bering seas. Density estimates for those same eight groups (bivalves, snails, sea stars, brittle stars, urchins-dollars-cucumbers, benthic amphipods, polychaetes, and worms etc.) in the updated model are derived from benthic survey data (grab samples and beam trawls) gathered only in the eastern Chukchi Sea, and resulted in generally lower biomass estimates. The biomass estimates used in the updated model are region-specific and therefore have a higher data pedigree (2) than the biomass estimates used in the preliminary model (7).

The biomass of jellyfish (Schyphozoa) decreased by 43% from the preliminary model to the updated model. Both the biomass estimate in the preliminary model and the estimate we calculated here for the updated model are derived from bottom-trawl survey catch data and do not accurately estimate the total jellyfish biomass as jellies may be found throughout the water column, and are poorly sampled by bottom trawl gear. Though the two surveys used comparable trawling gear, the sampling design, total area surveyed, and total number of stations sampled differ between the two surveys. Additionally, the difference between the two biomass estimates may reflect interannual variation in species abundance, species composition, and spatial distribution. The two density estimates are merely point estimates and are not suitable for establishing any trend in biomass or abundance.

There was a small increase in the estimated aggregate biomass of zooplankton (copepods and other zooplankton). As these groups are top-down balanced, this gain in biomass reflects an overall (slight) increase in demand from predators. There is an equally small increase in the proportion of total system biomass represented by zooplankton (+0.2%). This is the net result of an overall decrease in total system biomass (excluding detritus) in combination with the small increase in zooplankton biomass. The decrease in total system biomass is largely driven by the 23% decrease in benthic-oriented invertebrates, which are not important consumers of zooplankton. The consumptive demand for zooplankton from predators in the updated model is sufficient to maintain biomass levels roughly equivalent to their values in the preliminary model.

Similar to zooplankton, the aggregate biomass of microbes decreased 4% from the preliminary model to the updated model. As these groups are also top-down balanced, this reduction in biomass reflects a net decrease in demand from predators. However, the proportion of total system biomass represented by microbes increased by 1.2% from the preliminary model to the updated model. This is primarily the result of a decrease in total system biomass (down 18%) that is proportionally greater than the decrease in microbe biomass (down 4%).

The estimated biomass of phytoplankton decreased 18% from the preliminary model (34 t km^{-2}) to the updated model (27.8 t km^{-2}). This is directly related to our method for balancing benthic detritus by supplementing the benthic detrital pool with phytodetritus (i.e., increasing phytoplankton biomass). The amount of organic material required to balance the benthic pool is directly related to the trophic demand for benthic detritus from benthic detritivores. Because the estimated biomass of benthic detritivores decreased from the preliminary to the updated model, so did the trophic demand for benthic detritus. This resulted in a lower amount of phytodetritus required to balance the benthic detrital pool in the updated model, and ultimately a lower biomass estimate for phytoplankton.

Ecosystem metrics

The ecosystem-level metrics highlight a few key differences between the preliminary model and our updated model. In general, the preliminary model had more biomass, production, and total flow than the updated model (Table 13). Changes to these ecosystem-scale metrics can largely be traced back to changes in input parameters that improved several data pedigrees. The 23% decrease in benthic-oriented invertebrate biomass had the most profound effect on these ecosystem metrics. The improved data used to estimate benthic-oriented invertebrate biomass improved the data pedigree for most of these groups from 7 to 2, but ultimately resulted in lower biomass estimates. Benthic invertebrates dominate this ecosystem in terms of biomass, and the total reduction in their biomass estimates (65.3 t km^{-2}) is approximately equal to the reduction in total system biomass from the preliminary model (355.5 t km^{-2}) to the updated model (291.1 t km^{-2}). Increases in biomass for mammals, seabirds, fish, and zooplankton (combined increase of 8.3 t km^{-2}) are similar in magnitude to biomass decreases for jellyfish, microbes, and phytoplankton (combined decrease of 7.4 t km^{-2}, Table 13).

The reduction in benthic invertebrate biomass also affects the reduction in total production (Table 13). Because many of these benthic invertebrates with lower biomass estimates are important consumers of benthic detritus, and benthic detritus is balanced by supplementing the benthic detrital pool with phytodetritus, the reduction in benthic invertebrate biomass ultimately resulted in lower phytoplankton biomass in the updated model than in the preliminary model. This resulted in lower total primary production and ultimately lower total ecosystem production. The reduction in net primary production from the preliminary model (2,550 t km^{-2} yr^{-1}) to the updated model (2,085 t km^{-2} yr^{-1}) accounts for ~80% of the reduction in total ecosystem production between these two models. Additionally, the lower biomass estimates of benthic invertebrates in combination with changes to several of their P/B rates resulted in a net loss in production of these groups, accounting for ~16% of the loss in total system production in the updated model. Overall, the total production in the updated model is about 16% lower than in the preliminary model.

Total system throughput measures the total mass flow in an ecosystem and reflects the overall size of the ecosystem (Christensen et al. 2005). Total system throughput in the updated model is about 15% lower than in the preliminary model and is a reflection of the combined decreases in biomass and production. Not coincidentally, the size of reduction in total system throughput is similar in magnitude to the reductions seen in total biomass (-18%), production (-16%), and net primary production (-18%). The decreases in biomass and production reduce the mass flow rates for consumption, respiration, and flow to detritus, ultimately lowering the total system throughput.

Overall, the fundamental structure and function of the preliminary model is maintained in the updated model (Figures 3 and 4). The majority of biomass is found in benthic invertebrate groups, and mass flows are dominated by flows from benthic sources (blue boxes in Figures 3 and 4). The combined changes in total ecosystem production and total biomass resulted in a modest ~2% increase in the ratio of total production to total biomass. The total ecosystem P/B is 10.3 in the updated model, up from 10.1 in the preliminary model. Despite the numerous small changes to input parameter values that resulted in substantial decreases in total biomass, production, and net primary production, the relatively unchanged state of the ecosystem P/B reflects the maintenance of key structural and functional properties from the preliminary model in the updated model.

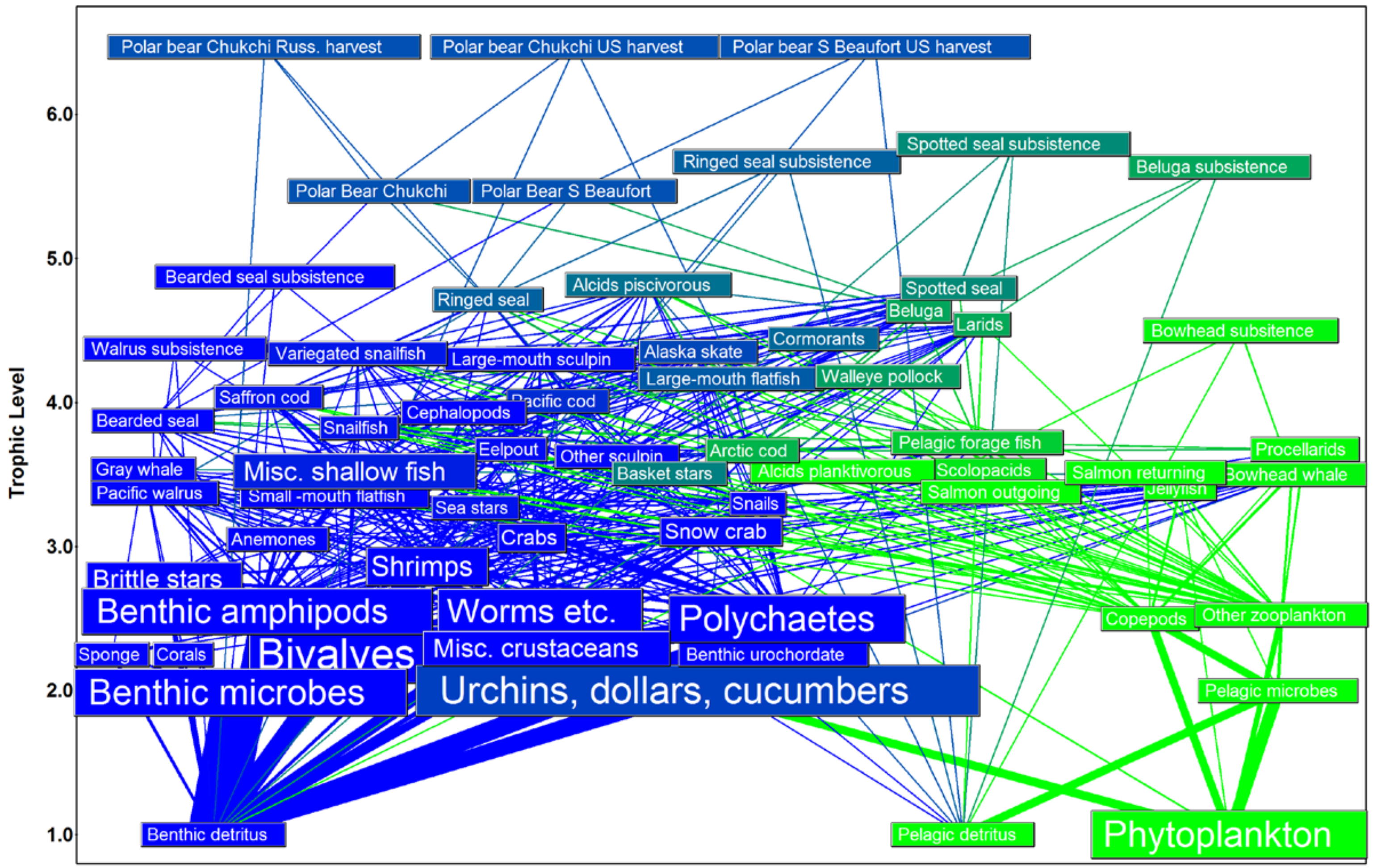

Figure 3. -- Food web diagram of the updated eastern Chukchi Sea food web (~2012). Functional groups (boxes) are arranged vertically by trophic level (a few groups are staggered up or down to improve readability). The height of the box is roughly proportional to the log biomass of the group. The width of the line between groups is proportional to the magnitude in mass flow. Blue boxes highlight benthic basal resources, and green boxes highlight pelagic sources, with a gradient of shades in between.

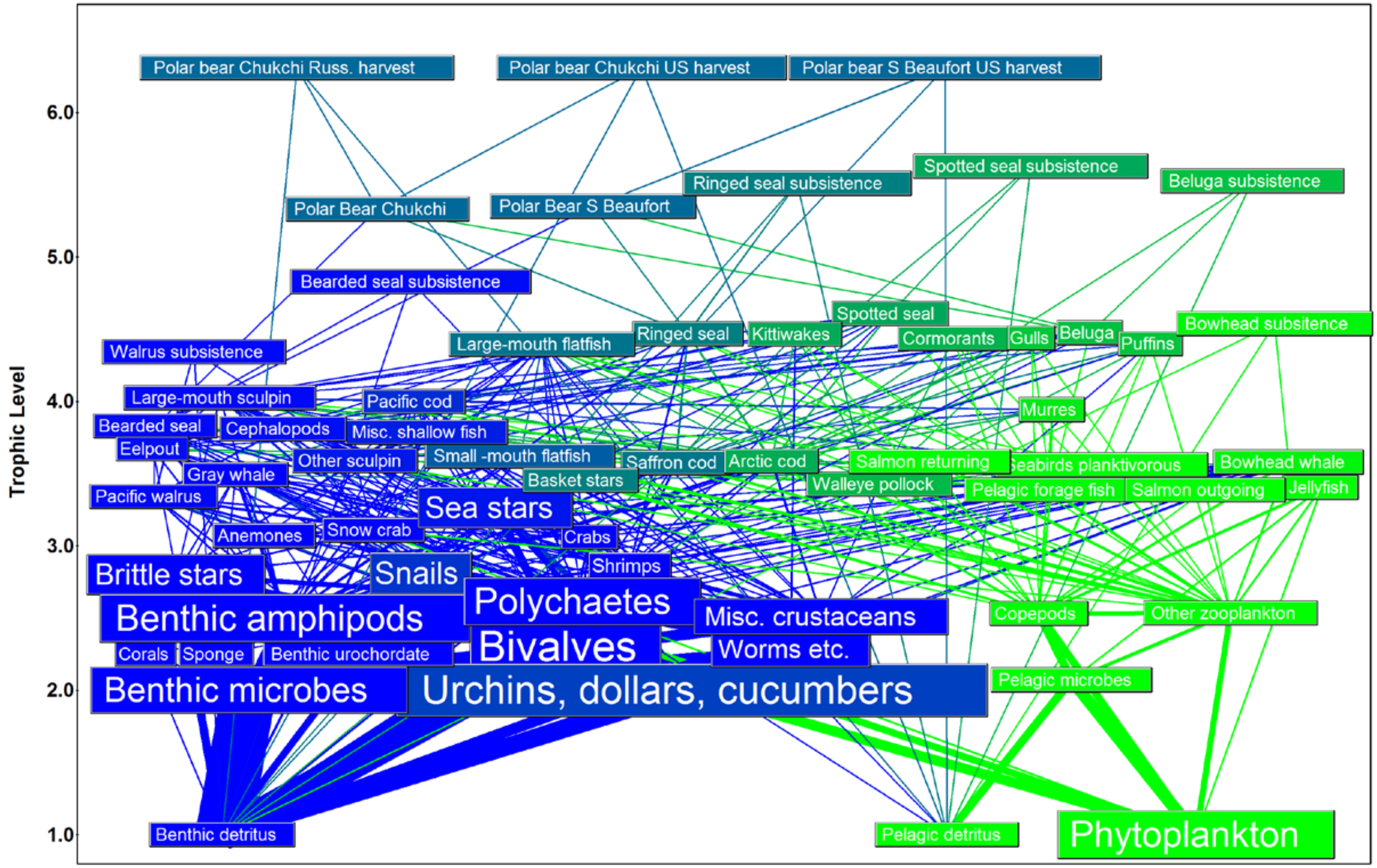

Figure 4. -- Food web diagram of the preliminary eastern Chukchi Sea food web (~1990). Functional groups (boxes) are arranged vertically by trophic level (a few groups are staggered up or down to improve readability). The height of the box is roughly proportional to the log biomass of the group. The width of the line between groups is proportional to the magnitude in mass flow. Blue boxes highlight benthic basal resources, and green boxes highlight pelagic sources, with a gradient of shades in between.

DISCUSSION

It is unclear whether any differences in Ecopath model properties and food web metrics between the preliminary model base time period (~1990) and the present model update (~2012) reflect any change in the true ecosystem conditions. Virtually all differences in model metrics and outputs can be traced to changes to model inputs, reflecting new and improved data (i.e., higher data pedigree). To properly evaluate changes across time would require an adequate time series of data that connects the two model time periods (1990 to 2012). The two models are more appropriately viewed as two benchmarks, using many different data and parameter sources, and separated by about 20 years. Overall, the fundamental structure and function of the two models are the same; the system is dominated by benthic invertebrates and we observed little change in the ecosystem metrics and the proportions of total biomass represented by the aggregated groups.

A key limitation of both the preliminary model and the present model update is the seasonal nature of most of the data sets used to parameterize the models. The southward advance of sea ice during fall makes accessing the Alaska Arctic for fieldwork extremely difficult and costly, not to mention cold and dark. Offshore field studies during winter months are confined to a limited number of vessels with ice-breaking capacity. As a result, much of the offshore marine field research in the Alaska Arctic has been performed between spring and fall, and much of the data this trophic model is based upon reflects summer conditions. Until winter fieldwork becomes more feasible or the environmental conditions (sea ice reduction) allow more winter fieldwork, this is a limitation on the available data sets. For those model parameters that are derived from summer data sets we are making the assumption that conditions do not appreciably change during winter months, though this is certainly untrue in many cases (e.g., primary and secondary production). For example there is a strong seasonal signal with summer peaks in primary production (Springer and McRoy 1993) and secondary production of pelagic invertebrates (Matsuno et al. 2011, Questel et al. 2013). Future fieldwork emphasizing winter data collections would help to address this shortcoming for resident species present in the Chukchi Sea year-round. However, cost and logistical challenges will likely persist and continue to limit winter collections.

The static Ecopath framework assumes a spatially homogenous model and does not address spatial differences in biomass or species composition. The community compositions of seabirds, fishes, and benthic invertebrates are all known to be spatially variable in the eastern Chukchi Sea and related to spatially varying oceanographic conditions (Norcross et al. 2010, Day et al. 2013, Gall et al. 2013, Norcross et al. 2013, Blanchard and Feder 2014). Patterns in the spatial distribution of zooplankton species have also been linked with distinct water masses and environmental variables (Springer et al. 1989, Hopcroft et al. 2010, Questel et al. 2013, Pinchuk and Eisner In press). Primary production is also spatially variable and associated with sea ice phenology and distinct water masses (Hansell et al. 1993, Springer and McRoy 1993). Spatial variation in community composition and biomass would likely lead to spatial variation in food web structure. In the southern Chukchi Sea, Iken et al. (2010) found the structure of the benthic food web to vary depending upon the overlying water mass. Given the observed spatial differences in primary production and species distributions, future modeling efforts addressing these spatial patterns may find the food webs to have similar spatial variability. For example, in the south-central Chukchi Sea where primary production is high, there is strong pelagic-benthic coupling, and high benthic biomass (Grebmeier et al. 1988); we may hypothesize that in this area the food web structure and energy flow would be dominated by benthic organisms. In contrast, in coastal waters of the Chukchi Sea where primary production and benthic biomass is generally lower (Dunton et al. 2005), food web structure may be more balanced between pelagic and benthic basal resources. Future food web modeling with a spatially explicit framework (e.g., Ecospace) could help to reveal such patterns in food web structure and could be informative for describing predator spatial distributions.

Fish

An important outcome of both the preliminary model and the present model update is that survey-derived estimates of fish biomass were insufficient to balance either of the models and fish biomass needed to be increased substantially to meet the estimated demand by predators. This result implies that some portion of the fish biomass is unavailable to the fish sampling gear or the locations surveyed, or that the Ecopath model overestimates fish biomass. Though it is possible that some portion of the fish biomass is unavailable, there are several possible explanations that may help explain the apparent underestimation of fish biomass by the trawl survey. Low biomass in the trawl survey data may reflect low catchability of some groups to the bottom trawl gear, particularly pelagic fish. Large mesh size may have permitted smaller fishes to escape capture. Additionally, fish may be patchily distributed and not encountered by the trawl. The survey-derived estimates reflect just a single year, and interannual variation in fish abundance may have contributed to an underestimation of fish biomass. Further, any imprecision in the predator diets included in the model, or overestimation of predator biomass and consumptive rates, would have additionally contributed to the mismatch in biomass estimates between the trawl-derived estimates (EBT and beam-trawl) and the top-down forced Ecopath estimate.

At 40 of the 2012 Arctic Eis sampling stations both bottom trawling gears were used. The catch data from these gear comparison tows indicated differences in the catch data between the two gear types and may reflect differences in gear design and performance (Britt et al. 2013). A greater abundance of smaller fish and smaller benthic invertebrates, including infauna typically found just below the surface, was observed in the beam trawl catch and is thought to reflect the finer mesh size in the beam trawl and a tendency to scour the bottom harder than the EBT (Britt et al. 2013). The size composition of fishes and snow crabs caught with the EBT were generally larger than those caught with the beam trawl. The EBT was more efficient at catching larger and more mobile organisms, including those found just above the seafloor, due to its greater net width, higher vertical opening, and higher towing speed (Britt et al. 2013).

When we compare biomass estimates calculated for our Ecopath fish functional groups from the two gear types a few differences in the data become apparent (Figure 5). The EBT gear produced higher biomass estimates for gadids, pelagic forage fish, and Alaska skate. The beam trawl produced higher density estimates for miscellaneous shallow fish, snailfish, sculpins, and small-mouth flatfish. The most pronounced difference was for the miscellaneous shallow fish group, where the beam trawl estimate was 0.333 t km^{-2} and the EBT was 0.004 t km^{-2}. This may reflect actual differences in the density of miscellaneous shallow fishes encountered by the two gears, but may also reflect differences in gear design (e.g., mesh size) and performance (e.g., harder contact with the bottom). The miscellaneous shallow fish group is dominated by stichaeids (e.g., pricklebacks, eelblennys) which are generally small and slender fish that could escape through net meshes or pass under a foot rope. Though the two gears may have in fact encountered different densities of miscellaneous shallow fish, it is also possible that differences in mesh size and bottom contact, contributed to the disparity in biomass estimates for this functional group.

The top-down forced estimates of biomass for the fish functional groups calculated by Ecopath are in general significantly larger than the estimates derived from the trawl survey catch data. The disparity between these different estimates makes it difficult to visually compare them side-by-side (Figure 6). Alternatively, we can look at the proportions of the fish groups relative to total fish biomass to gain a sense of any differences in the distribution of biomass amongst the fish functional groups. We can accomplish this by summing up the fish biomass estimates and dividing each group by this total to determine a group's contribution to total fish biomass. Figure 7 shows the relative fish proportions for the EBT, beam trawl, and Ecopath estimates side-by-side. The most conspicuous result is that both the Ecopath output and the beam trawl data indicate the relative prominence of miscellaneous shallow fish amongst all fish groups. This observation supports the notion that the EBT may have undersampled the miscellaneous shallow fish group and that the beam trawl correctly indicated the prominence of this functional group. Or rather, the beam trawl data are consistent with the Ecopath results suggesting the prominence of this functional group amongst fish groups. Miscellaneous shallow fish, in particular stichaeids, were a prominent prey item commonly observed in the diets of piscivorous fishes in the eastern Chukchi Sea (Whitehouse et al. In press). Because the biomass estimate of miscellaneous shallow fishes is forced by top-down pressure, the high proportion of miscellaneous shallow fish amongst all other fish groups in the Ecopath model is in large part a reflection of their dietary importance as prey to other piscivorous fishes.

Another noteworthy contrast is the difference in the proportion of pelagic forage fishes (Figure 7). The bottom trawl catch data indicates this group to be among the more prominent groups while they are barely represented in the beam trawl catch. The proportion of pelagic fish from the top-down estimate of Ecopath is intermediate between these two estimated proportions. The disparity in the proportions from the two sets of trawl data may reflect the low catchability of this group to bottom trawling gear in general. The higher density estimate from the EBT data may be a result of the higher vertical opening of the net and higher trawling speed.

Some conspicuous contrasts in Figure 7 are the different proportions for Arctic cod and saffron cod. The relative proportions of Arctic cod and saffron cod are greatest in the bottom trawl data. They are the two most prominent portions (functional groups) of the fish community in the EBT data. The proportion of Arctic cod in the beam trawl data is less than half that of the bottom trawl, but roughly equivalent to the proportion estimated with the Ecopath model. The relative proportion of Arctic cod ranks fifth amongst the fish groups from the beam trawl data. For saffron cod, they are scarcely represented in the beam trawl data, while the Ecopath proportion of saffron cod is intermediate between the EBT and beam trawl estimates. Differences in the relative proportions of gadids between the two trawling gears may reflect actual differences in the densities of gadids encountered, and patchy fish distribution (trawling locations), and likely reflect different efficiencies between the two gears to catch Arctic cod and saffron cod (Britt et al. 2013). Recent studies employing the same EBT gear in the eastern Bering Sea have shown the effective fishing height of the EBT for another species of Gadidae, the walleye pollock, to be greater than the measured vertical opening of the net (Kotwicki et al. 2013).

In general, the overall pattern of biomass dominance by the miscellaneous shallow fish group in the Ecopath model results is supported by a similar pattern observed in the beam trawl data (Figure 7). Though the biomass estimate produced by Ecopath for miscellaneous shallow fish is considerably higher than the biomass estimates calculated by either gear types (EBT and beam), the pattern of biomass dominance by this group is consistent with the pattern we observe in the beam trawl catch. Given the slender shape and small size of many of the miscellaneous shallow fishes (e.g., stichaeids), and taking differences in the design and performance of the two gear types into consideration, this functional group of fishes may have been more efficiently caught with the beam trawl and could be underrepresented in the EBT catch. The vast differences between the dimensions, performance, and catches of the two gear types make statistical comparisons impracticable at this time (Britt et al. 2013). The top-down forced biomass estimate of miscellaneous shallow fish generated by the Ecopath model is largely driven up by top-down pressure from other fishes. The diets of those predator fishes included in the present model update are derived from fish stomachs that were collected in the eastern Chukchi Sea during the 2012 Arctic Eis trawl surveys.

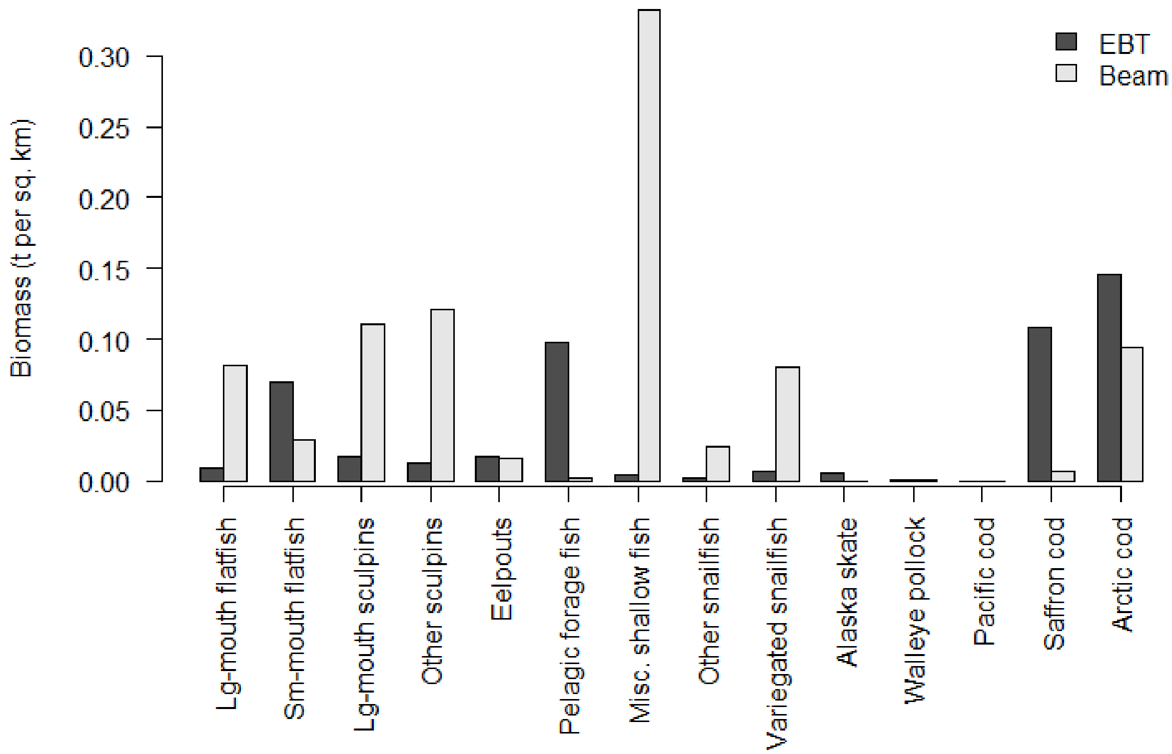

Figure 5. -- Biomass estimates (t km-2) for fish functional groups (excluding salmonids) derived from the catch data of the 83-112 Eastern bottom trawl (EBT) and the beam trawl.

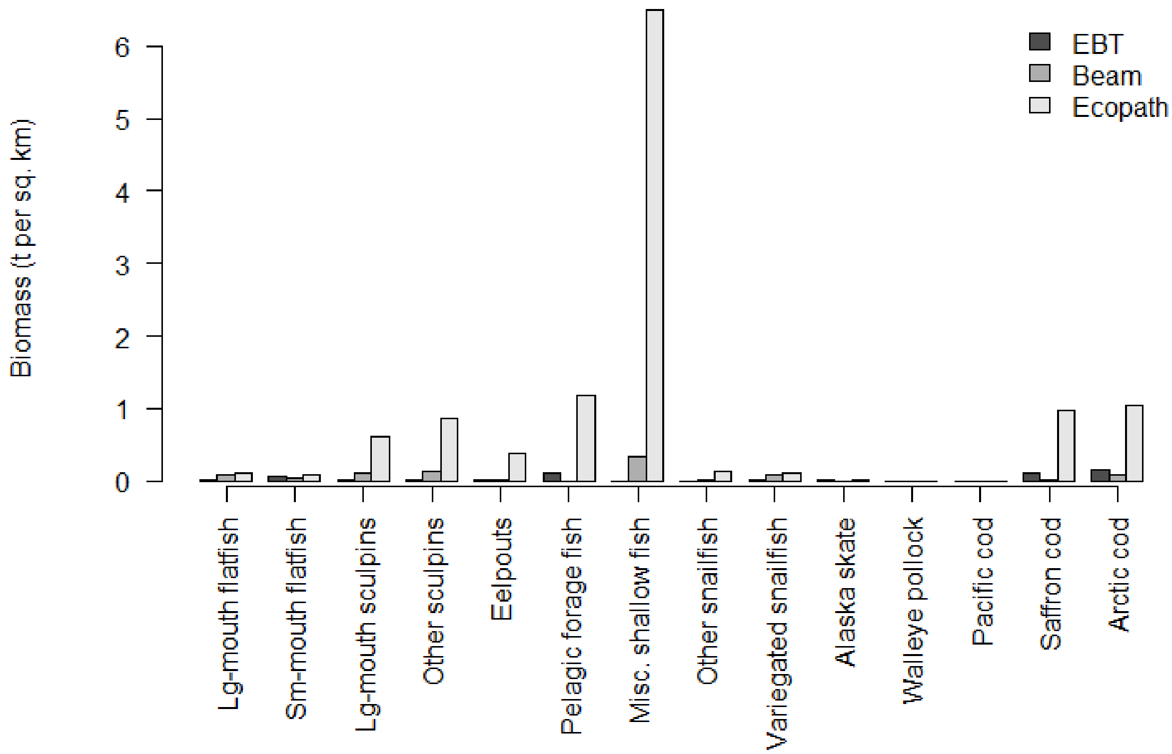

Figure 6. -- Biomass estimates (t km^{-2}) for fish functional groups (excluding salmonids) derived from the catch data of the 83-112 Eastern bottom trawl (EBT), the catch data from the beam trawl, and the biomass estimates produced by Ecopath, assuming EE = 0.8.

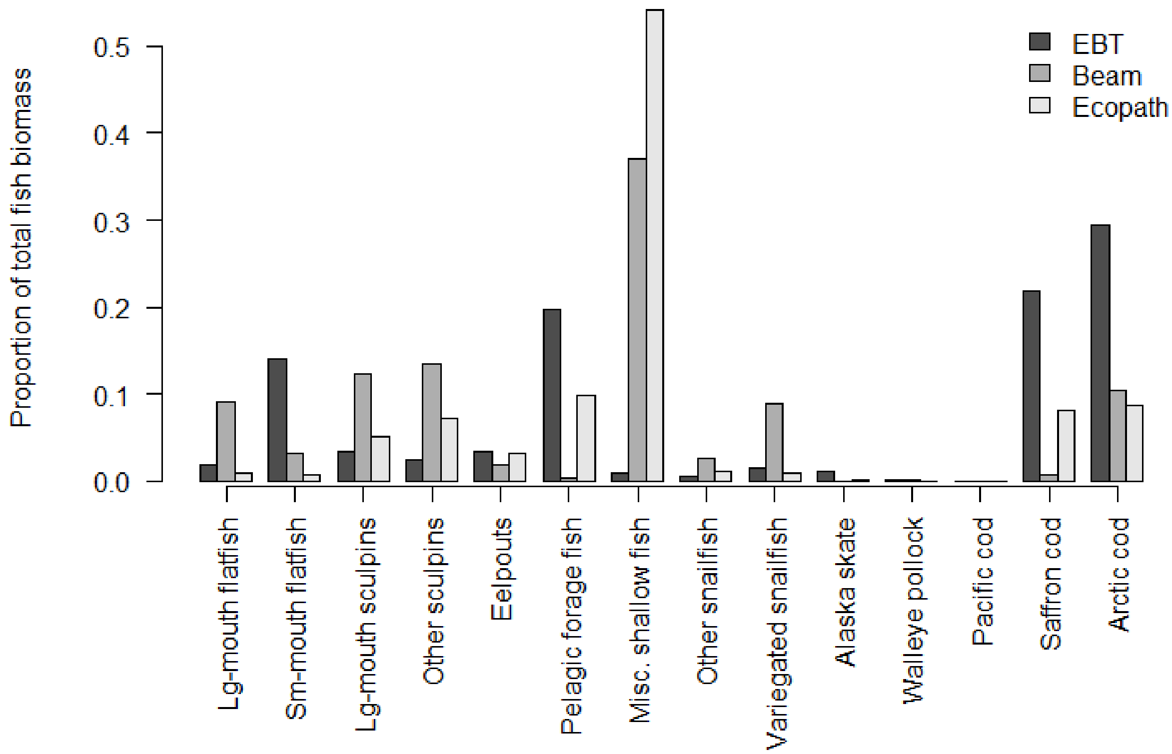

Figure 7. -- The proportional contribution of fish functional groups to the combined biomass of all fish groups (excluding salmonids) using three different estimates of biomass; the catch data from the 83-112 Eastern bottom trawl (EBT), the beam trawl, and the biomass estimates produced by Ecopath (assuming EE = 0.8).

CONCLUSIONS

We were able to update or otherwise improve (data pedigree) input parameter estimates for numerous functional groups. Despite all of the changed input parameters, the fundamental structure and function of this trophic mass balance model of the eastern Chukchi Sea remains the same as that of the original preliminary model. The eastern Chukchi Sea is an ecosystem characterized by strong pelagic-benthic coupling, where a large portion of the primary production within the pelagic realm is unutilized in the pelagic food web and most of it eventually settles to the seafloor where it supports an abundant benthic community. A large majority of the living biomass in this ecosystem resides in the benthic community.

Similar to the preliminary model, survey-derived estimates of fish biomass were insufficient to balance the model, and top-down estimates indicate fish biomass may be much higher than the survey-derived estimates. Small demersal fishes, especially pricklebacks, may represent a significant portion of total fish biomass and may be underestimated by trawl survey-derived estimates.

In general, changes to key model parameters, such as biomass, or changes to system level metrics, were the reflection of the new and improved data or parameters used as model inputs, and do not necessarily reflect any change in ecosystem (or functional group) state from the preliminary model (~1990) to our updated model (~2012). The two models are analogous to two data points in time and are not equivalent to a time series. A more rigorous analysis of available time series data for individual functional groups will be required to evaluate changes over time.

We updated 93 of the 227 basic model input parameters (B, P/B, Q/B, EE, GE, DC, C), which resulted in improved data pedigrees for 34 of the input parameters. Given the improvements to input parameter quality and the more current base time period of this model update(~2012 vs. ~1990), we recommend the use of this updated model over the preliminary model for future food web modeling studies, including simulation and sensitivity analyses with Ecosim, or spatially explicit studies with Ecospace (Pauly et al. 2000).

Our food web model represents just one of many possible mass-balanced states (Essington 2004). The table of data quality grades for the basic model input parameters (Appendix B) highlighted the many parameters in need of improved estimates and may help to direct future research and field collections. Regular updates to food web models (every ~3-5 years), such as ours, can support the calculation of informative ecosystem indicators, help to identify ecologically important species still in need of further research, and aid in the identification of trends and changes to the trophic structure and functioning of an ecosystem (Aydin et al. 2007).

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APPENDIX A

Diet Matrix

Appendix Table A1. -- The diet matrix of the updated eastern Chukchi Sea Ecopath model. Rows represent prey groups and the columns are predators. The predator column numbers correspond to the prey group numbers and names. Each column represents a single predator's diet and the values sum to 1 (some columns may not sum to 1 due to rounding). Values of 0.0000 are prey items present in trace amounts.

Appendix Table A1. -- Cont.

	Functional Group	1	2	3	4	5	6	7	8
1	Beluga				0.1000	0.1000			
2	Gray whale								
3	Bowhead whale								
4	Polar bear Chukchi								
5	Polar bear S Beaufort								
6	Pacific walrus								
7	Bearded seal				0.2500	0.2500	0.0003		
8	Ringed seal				0.6500	0.6500	0.0007		
9	Spotted seal								
10	Procellarids								
11	Cormorants								
12	Scolopacids								
13	Larids								
14	Alcids piscivorous								
15	Alcids planktivorous								
16	Large-mouth flatfish							0.0215	
17	Small -mouth flatfish							0.0215	
18	Large-mouth sculpin	0.0100						0.0586	0.0331
19	Other sculpin	0.0100							0.0069
20	Eelpout	0.0100							
21	Pelagic forage fish	0.5544						0.0023	0.0300
22	Misc. shallow fish								
23	Other snailfish								
24	Variegated snailfish								
25	Alaska skate								
26	Walleye pollock								
27	Pacific cod								
28	Saffron cod	0.0359						0.0180	0.3300
29	Arctic cod	0.2797						0.0085	0.4500
30	Salmon outgoing								
31	Salmon returning								
32	Cephalopods	0.0001					0.0100		
33	Bivalves		0.0434	0.0192			0.6990	0.3286	
34	Snails		0.0043	0.0019			0.0600	0.0170	
35	Snow crab		0.0003	0.0001			0.0230	0.1948	
36	Other crabs		0.0001	0.0000			0.0070	0.0601	
37	Shrimps	0.0999	0.0000	0.0000			0.0200	0.2464	0.1000
38	Sea stars		0.0040	0.0018					
39	Brittle stars		0.0037	0.0016					
40	Basket stars		0.0001	0.0001					
41	Urchins, dollars, cucumbers		0.0229	0.0102			0.0802		
42	Sponge		0.0002	0.0001					
43	Benthic urochordate		0.0026	0.0012			0.0092		
44	Anemones		0.0026	0.0012					
45	Corals		0.0000	0.0000					
46	Benthic amphipods		0.9000	0.0057			0.0448	0.0113	0.0400
47	Polychaetes		0.0109	0.0048			0.0380	0.0113	
48	Worms etc.		0.0022	0.0010			0.0078		
49	Misc. crustaceans		0.0026	0.0011					
50	Jellyfish								
51	Copepods			0.7125					
52	Other zooplankton			0.2375					0.0100
53	Pelagic microbes								
54	Benthic microbes								
55	Phytoplankton								
56	Pelagic detritus								
57	Benthic detritus								

Appendix Table A1. -- Cont.

	Functional Group	9	10	11	12	13	14	15	16
1	Beluga								
2	Gray whale								
3	Bowhead whale								
4	Polar bear Chukchi								
5	Polar bear S Beaufort								
6	Pacific walrus								
7	Bearded seal								
8	Ringed seal								
9	Spotted seal								
10	Procellarids								
11	Cormorants								
12	Scolopacids								
13	Larids								
14	Alcids piscivorous					0.0047			
15	Alcids planktivorous								
16	Large-mouth flatfish	0.0085					0.0096		
17	Small -mouth flatfish	0.0085					0.0096		
18	Large-mouth sculpin	0.1197				0.0017	0.0714		
19	Other sculpin	0.0247				0.0017	0.0713		
20	Eelpout								
21	Pelagic forage fish	0.4574	0.0587	0.2500		0.3325	0.2732		
22	Misc. shallow fish	0.0108		0.2500		0.0035	0.0033		0.3332
23	Other snailfish	0.0108				0.0035	0.0033		
24	Variegated snailfish	0.0108				0.0035	0.0033		
25	Alaska skate								
26	Walleye pollock								
27	Pacific cod								
28	Saffron cod	0.0924				0.0233	0.2372		
29	Arctic cod	0.2163	0.0697	0.2500		0.5013	0.2595		0.2409
30	Salmon outgoing								
31	Salmon returning								
32	Cephalopods	0.0200							
33	Bivalves					0.0000	0.0000		0.0073
34	Snails					0.0053	0.0030		
35	Snow crab								
36	Other crabs					0.0053	0.0030		
37	Shrimps	0.0100		0.2500		0.0106	0.0100		0.1977
38	Sea stars								
39	Brittle stars								
40	Basket stars								
41	Urchins, dollars, cucumbers								
42	Sponge								
43	Benthic urochordate								
44	Anemones								
45	Corals								
46	Benthic amphipods	0.0100	0.0022		0.1000	0.0345	0.0233		0.0252
47	Polychaetes					0.0237	0.0082		0.0497
48	Worms etc.								
49	Misc. crustaceans					0.0001			
50	Jellyfish							0.0193	
51	Copepods		0.0044		0.4500			0.3486	0.0000
52	Other zooplankton		0.8650		0.4500	0.0263	0.0108	0.6321	0.1459
53	Pelagic microbes								
54	Benthic microbes								
55	Phytoplankton								
56	Pelagic detritus					0.0056			
57	Benthic detritus					0.0130			

Appendix Table A1. -- Cont.

	Functional Group	17	18	19	20	21	22	23	24
1	Beluga								
2	Gray whale								
3	Bowhead whale								
4	Polar bear Chukchi								
5	Polar bear S Beaufort								
6	Pacific walrus								
7	Bearded seal								
8	Ringed seal								
9	Spotted seal								
10	Procellarids								
11	Cormorants								
12	Scolopacids								
13	Larids								
14	Alcids piscivorous								
15	Alcids planktivorous								
16	Large-mouth flatfish								0.0126
17	Small -mouth flatfish							0.0286	
18	Large-mouth sculpin				0.0480	0.0058		0.0164	0.0819
19	Other sculpin		0.2068		0.0008	0.0042		0.0120	0.1074
20	Eelpout		0.0893						0.0091
21	Pelagic forage fish			0.0373				0.0661	0.0323
22	Misc. shallow fish		0.2435		0.0788	0.1874			0.1844
23	Other snailfish		0.0035		0.0001				0.1430
24	Variegated snailfish		0.0113		0.0003			0.0586	
25	Alaska skate								
26	Walleye pollock								
27	Pacific cod								
28	Saffron cod								
29	Arctic cod								0.0120
30	Salmon outgoing								
31	Salmon returning								
32	Cephalopods								
33	Bivalves	0.3710		0.0014	0.0004		0.0539	0.0003	0.0037
34	Snails	0.0005		0.0068			0.0004		
35	Snow crab	0.0265	0.0753	0.0023				0.0131	0.0093
36	Other crabs	0.0002	0.1497	0.0573	0.0021	0.0003	0.0070	0.0350	0.0038
37	Shrimps		0.1319	0.0123	0.0155	0.0098	0.0773	0.1046	0.2867
38	Sea stars								
39	Brittle stars	0.0304	0.0000	0.0054					
40	Basket stars								
41	Urchins, dollars, cucumbers	0.0511							
42	Sponge								
43	Benthic urochordate								
44	Anemones			0.0638					
45	Corals								
46	Benthic amphipods	0.1203	0.0703	0.4825	0.2815	0.0134	0.5202	0.4949	0.0714
47	Polychaetes	0.3520	0.0105	0.2353	0.5377	0.0046	0.1270	0.1528	0.0288
48	Worms etc.	0.0083		0.0600			0.0149		0.0003
49	Misc. crustaceans	0.0368	0.0069	0.0075	0.0009	0.0006	0.0827	0.0053	0.0006
50	Jellyfish								
51	Copepods	0.0001			0.0000	0.3125	0.0179	0.0003	0.0000
52	Other zooplankton	0.0028	0.0008	0.0282	0.0340	0.4613	0.0987	0.0119	0.0126
53	Pelagic microbes								
54	Benthic microbes								
55	Phytoplankton								
56	Pelagic detritus								
57	Benthic detritus								

Appendix Table A1. -- Cont.

	Functional Group	25	26	27	28	29	30	31	32
1	Beluga								
2	Gray whale								
3	Bowhead whale								
4	Polar bear Chukchi								
5	Polar bear S Beaufort								
6	Pacific walrus								
7	Bearded seal								
8	Ringed seal								
9	Spotted seal								
10	Procellarids								
11	Cormorants								
12	Scolopacids								
13	Larids								
14	Alcids piscivorous								
15	Alcids planktivorous								
16	Large-mouth flatfish	0.0249		0.0015		0.0061			
17	Small -mouth flatfish	0.0643		0.0107					
18	Large-mouth sculpin	0.0236		0.0066		0.0063			
19	Other sculpin	0.0003		0.0049					
20	Eelpout	0.0413		0.0043		0.0036			
21	Pelagic forage fish	0.0528				0.0495			
22	Misc. shallow fish	0.0155		0.0635	0.3514	0.0021			
23	Other snailfish	0.0014		0.0007		0.0028			
24	Variegated snailfish	0.0040		0.0021					
25	Alaska skate								
26	Walleye pollock			0.0006					
27	Pacific cod	0.0014							
28	Saffron cod								
29	Arctic cod	0.2730	0.5367	0.1560		0.0082			
30	Salmon outgoing								
31	Salmon returning	0.0210							
32	Cephalopods	0.0001							
33	Bivalves	0.0000		0.0014	0.0000	0.0000			0.2500
34	Snails	0.0001		0.0015	0.0023				0.2500
35	Snow crab	0.2568		0.1453					0.2500
36	Other crabs	0.0608		0.0526	0.0006	0.0011			0.2500
37	Shrimps	0.1139	0.1424	0.2859	0.4781	0.1601			
38	Sea stars								
39	Brittle stars	0.0000							
40	Basket stars								
41	Urchins, dollars, cucumbers	0.0001							
42	Sponge								
43	Benthic urochordate	0.0002							
44	Anemones	0.0000							
45	Corals								
46	Benthic amphipods	0.0302	0.0430	0.1378	0.0380	0.0957			
47	Polychaetes	0.0074		0.0692	0.0336	0.0045			
48	Worms etc.				0.0597				
49	Misc. crustaceans	0.0001	0.0344	0.0015	0.0012	0.0120			
50	Jellyfish								
51	Copepods	0.0000	0.1473		0.0000	0.3725	0.5000	0.5000	
52	Other zooplankton	0.0066	0.0963	0.0539	0.0352	0.2756	0.5000	0.5000	
53	Pelagic microbes								
54	Benthic microbes								
55	Phytoplankton								
56	Pelagic detritus								
57	Benthic detritus								

Appendix Table A1. -- Cont.

	Functional Group	33	34	35	36	37	38	39	40
1	Beluga								
2	Gray whale								
3	Bowhead whale								
4	Polar bear Chukchi								
5	Polar bear S Beaufort								
6	Pacific walrus								
7	Bearded seal								
8	Ringed seal								
9	Spotted seal								
10	Procellarids								
11	Cormorants								
12	Scolopacids								
13	Larids								
14	Alcids piscivorous								
15	Alcids planktivorous								
16	Large-mouth flatfish								
17	Small -mouth flatfish								
18	Large-mouth sculpin								
19	Other sculpin								
20	Eelpout								
21	Pelagic forage fish								
22	Misc. shallow fish								
23	Other snailfish								
24	Variegated snailfish								
25	Alaska skate								
26	Walleye pollock								
27	Pacific cod								
28	Saffron cod								
29	Arctic cod								
30	Salmon outgoing								
31	Salmon returning								
32	Cephalopods								
33	Bivalves		0.5000	0.2075	0.2500	0.1500	0.5155	0.1250	
34	Snails			0.0326			0.0516		
35	Snow crab								
36	Other crabs			0.0411					
37	Shrimps								
38	Sea stars			0.0015					
39	Brittle stars			0.0590					
40	Basket stars								
41	Urchins, dollars, cucumbers			0.0081			0.2723		
42	Sponge			0.0028					
43	Benthic urochordate						0.0314		
44	Anemones			0.0012					
45	Corals								
46	Benthic amphipods		0.0500	0.0553		0.1500		0.1250	0.2500
47	Polychaetes		0.3000	0.2720	0.2500	0.1500	0.1292	0.1250	
48	Worms etc.		0.0500	0.0313	0.2500				
49	Misc. crustaceans		0.0500	0.0143		0.1500		0.1250	0.2500
50	Jellyfish								
51	Copepods								0.2500
52	Other zooplankton			0.0041					0.2500
53	Pelagic microbes								
54	Benthic microbes	0.2500							
55	Phytoplankton			0.0039					
56	Pelagic detritus								
57	Benthic detritus	0.7500	0.0500	0.2657	0.2500	0.4000		0.5000	

Appendix Table A1. -- Cont.

	Functional Group	41	42	43	44	45	46	47	48
1	Beluga								
2	Gray whale								
3	Bowhead whale								
4	Polar bear Chukchi								
5	Polar bear S Beaufort								
6	Pacific walrus								
7	Bearded seal								
8	Ringed seal								
9	Spotted seal								
10	Procellarids								
11	Cormorants								
12	Scolopacids								
13	Larids								
14	Alcids piscivorous								
15	Alcids planktivorous								
16	Large-mouth flatfish								
17	Small -mouth flatfish								
18	Large-mouth sculpin								
19	Other sculpin								
20	Eelpout								
21	Pelagic forage fish								
22	Misc. shallow fish								
23	Other snailfish								
24	Variegated snailfish								
25	Alaska skate								
26	Walleye pollock								
27	Pacific cod								
28	Saffron cod								
29	Arctic cod								
30	Salmon outgoing								
31	Salmon returning								
32	Cephalopods								
33	Bivalves				0.2000				
34	Snails								
35	Snow crab								
36	Other crabs								
37	Shrimps								
38	Sea stars								
39	Brittle stars								
40	Basket stars								
41	Urchins, dollars, cucumbers								
42	Sponge								
43	Benthic urochordate								
44	Anemones								
45	Corals								
46	Benthic amphipods				0.2000				
47	Polychaetes								
48	Worms etc.								
49	Misc. crustaceans				0.2000				
50	Jellyfish								
51	Copepods								
52	Other zooplankton								
53	Pelagic microbes								
54	Benthic microbes		0.2500	0.2500	0.2000	0.2500	0.5000	0.5000	0.5000
55	Phytoplankton	0.2500							
56	Pelagic detritus								
57	Benthic detritus	0.7500	0.7500	0.7500	0.2000	0.7500	0.5000	0.5000	0.5000

Appendix Table A1. -- Cont.

	Functional Group	49	50	51	52	53	54
1	Beluga						
2	Gray whale						
3	Bowhead whale						
4	Polar bear Chukchi						
5	Polar bear S Beaufort						
6	Pacific walrus						
7	Bearded seal						
8	Ringed seal						
9	Spotted seal						
10	Procellarids						
11	Cormorants						
12	Scolopacids						
13	Larids						
14	Alcids piscivorous						
15	Alcids planktivorous						
16	Large-mouth flatfish						
17	Small -mouth flatfish						
18	Large-mouth sculpin						
19	Other sculpin						
20	Eelpout						
21	Pelagic forage fish						
22	Misc. shallow fish						
23	Other snailfish						
24	Variegated snailfish						
25	Alaska skate						
26	Walleye pollock						
27	Pacific cod						
28	Saffron cod						
29	Arctic cod						
30	Salmon outgoing						
31	Salmon returning						
32	Cephalopods						
33	Bivalves						
34	Snails						
35	Snow crab						
36	Other crabs						
37	Shrimps						
38	Sea stars						
39	Brittle stars						
40	Basket stars						
41	Urchins, dollars, cucumbers						
42	Sponge						
43	Benthic urochordate						
44	Anemones						
45	Corals						
46	Benthic amphipods						
47	Polychaetes						
48	Worms etc.						
49	Misc. crustaceans						
50	Jellyfish						
51	Copepods		0.6750		0.2500		
52	Other zooplankton		0.2250				
53	Pelagic microbes		0.0500	0.5000	0.1500		
54	Benthic microbes	0.5000					
55	Phytoplankton		0.0500	0.5000	0.6000	0.7000	
56	Pelagic detritus					0.3000	
57	Benthic detritus	0.5000					1.0000

APPENDIX B

Data Pedigree

Appendix Table B1. -- Data characteristics and data pedigree for the basic model input parameters. To aid the interpretation of parameter quality, the grades are color coded with light red as good (1-3), medium red as acceptable (4-6), and dark red as poor (7-8). *The Chukchi Sea stock of polar bears has two separate subsistence harvests (U.S. and Russian) that were parameterized separately. The data grade for the U.S. harvest is 2, and 7 for the Russian harvest. B = biomass,
P/B = production/biomass ratio, Q/B = consumption/biomass ratio, DC = diet composition, and C = fishery catch or subsistence harvest.

Appendix Table B1. -- Cont.

Model parameter	B		P/B		Q/B		DC		C	
Functional Group	**Grade**	**Data characteristics**	**Grade**	**Data characteristics**	**Grade**	**Data characteristics**	**Grade**	**Data characteristics**	**Grade**	**Data characteristics**
Beluga	5	Region-specific but required extrapolation based on migration patterns	6	General life history proxy	6	General life history proxy	5	Same species and same region	5	Estimate requires extrapolation and uncertain scaling factors
Gray whale	5		6		6		5			
Bowhead whale	5		6		6		5		2	Direct estimate with limited coverage
Polar bear Chukchi stock	7	Incomplete sources with wide range	5	Estimate based on same species	6		6	Same species in adjacent region	7* 2*	Single incomplete source Direct estimate with limited coverage
Polar bear S. Beaufort stock	5	Region-specific but required extrapolation based on migration patterns	4	Direct estimate	6		4	Direct estimate with limited coverage	2	Direct estimate with limited coverage
Pacific walrus	5		6	General life history proxy	6		5	Same species and same region	4	Direct estimate but with high variation/limited confidence
Bearded seal	7	Incomplete sources with wide range	6		6		4	Direct estimate with limited coverage	4	
Ringed seal	6	Single study with limited coverage	6		6		4		4	
Spotted seal	7	Incomplete sources with wide range	6		6		4		5	Estimate requires extrapolation and uncertain scaling factors
Procellarids	4	Direct estimate but with high variation/limited confidence	6		6		6	Same species in other regions		
Cormorants	4		6		6		6			
Scolopacids	4		6		6		6			
Larids	4		6		6		6			
Alcids piscivorous	4		6		6		6			
Alcids planktivorous	4		6		6		6			
Large-mouth flatfish	8	Estimated by Ecopath	5	Same species, different time period	5	Same species, different time period	2	Direct estimate with limited coverage		
Small-mouth flatfish	8		6	General life history proxy or other Ecopath model	6	General life history proxy or other Ecopath model	2			
Large-mouth sculpin	8		6		6		2			
Other sculpin	8		6		6		2			
Eelpout	8		6		6		2			
Pelagic forage fish	8		6		6		2			
Miscellaneous shallow fish	8		6		6		2			
Other snailfish	8		6		6		2			
Variegated snailfish	8		6		6		2			

Appendix Table B1. -- Cont.

Model parameter	B		P/B		Q/B		DC		C	
Functional Group	**Grade**	**Data characteristics**	**Grade**	**Data characteristics**	**Grade**	**Data characteristics**	**Grade**	**Data characteristics**	**Grade**	**Data characteristics**
Alaska skate	2	Direct estimate with limited coverage	6	General life history proxy or other Ecopath model	7	General literature review from a range of species	6	Same species in adjacent region		
Walleye pollock	2		6		6	General life history proxy or other Ecopath model	2	Direct estimate with limited coverage		
Pacific cod	2		6		6		6	Same species in adjacent region		
Saffron cod	8	Estimated by Ecopath	2	Direct estimate with limited coverage	2	Direct estimate with limited coverage	2	Direct estimate with limited coverage		
Arctic cod	8		2		2		2			
Salmon outgoing	7	Incomplete sources with wide range	6	General life history proxy or other Ecopath model	6	General life history proxy or other Ecopath model	6	Same species in adjacent region		
Salmon returning	7		6		6		6			
Cephalopods	8	Estimated by Ecopath	6		7	General literature review from a range of species	7	General literature review from a range of species		
Bivalves	2	Direct estimate with limited coverage	5	Species specific	7		7			
Snails	2		6	General life history proxy or other Ecopath model	7		7			
Snow crab	2		6		6	General life history proxy or other Ecopath model	6	Same species in adjacent region		
Miscellaneous crabs	2		6		7	General literature review from a range of species	7	General literature review from a range of species		
Shrimps	8	Estimated by Ecopath	6		7		7			
Sea stars	2	Direct estimate with limited coverage	6		7		7			
Brittle stars	2		6		7		7			
Basket stars	2		6		7		7			
Urchins, dollars, cucumbers	2		5	Species specific	7		7			
Sponge	2		6	General life history proxy or other Ecopath model	7		7			
Benthic urochordate	2		6		7		7			
Anemones	2		6		7		7			
Corals	2		6		7		7			
Benthic amphipods	8	Estimated by Ecopath	6		7		7			
Polychaetes	2	Direct estimate with limited coverage	5	Species specific	7		7			
Worms etc.	2		6	General life history proxy or other Ecopath model	7		7			
Miscellaneous crustaceans	2		6		7		7			
Jellyfish	2		6		6	General life history proxy or other Ecopath model	7			
Copepods	8	Estimated by Ecopath	6		6		7			
Other zooplankton	8		6		7	General literature review from a range of species	7			
Pelagic microbes	8		7	General literature review from a range of species	7		6	Same species and same region		
Benthic microbes	8		7		7		7	General literature review from a range of species		
Phytoplankton	8		7							
Pelagic detritus	8									
Benthic detritus	8									

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